

Review of the Genus *Hallaxa* (Nudibranchia: Actinocyclusidae) with Descriptions of Nine New Species

by

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Abstract. The genus *Hallaxa* previously included five described species. This paper describes nine new species of *Hallaxa*, and reviews the morphology of three of the previously described species. *Hallaxa atrotuberculata*, *H. albopunctata*, *H. iju*, *H. elongata*, *H. translucens*, *H. paulinae*, *H. hileenae*, and *H. cryptica* are described from the Indo-Pacific tropics, while *H. michaeli* is from the temperate east coast of Australia. The anatomy of an additional Indo-Pacific species is described, but the species is not named, as it is known only from preserved material. The polarity of characters is evaluated and a preliminary phylogeny is presented. The relationship of *Hallaxa* to *Actinocyclus*, the Chromodorididae, and other doridaceans is discussed.

INTRODUCTION

The genus *Hallaxa* Eliot, 1909, was originally erected to include two species, *H. decorata* (Bergh, 1878) and *H. indecora* (Bergh, 1905), both from the Indo-Pacific tropics. Subsequently, three species have been described, all from subtropical and temperate regions: *Hallaxa apesfiae* Marcus, 1957, from the subtropical coast of Brazil, *H. chani* Gosliner & Williams, 1975, from the Pacific coast of North America; and *H. gilva* Miller, 1987, is known from New Zealand.

Recent collections by several workers in the Indo-Pacific tropics have included specimens of several new species of *Hallaxa* (Figure 1). This paper describes the morphology of these species, as well as an additional species from temperate Australia, and reviews the anatomy of several previously described species. This review also permits a discussion of morphological variation in *Hallaxa* and a preliminary phylogenetic analysis.

Material from several institutions was examined during this study. Abbreviations for these institutions are as fol-

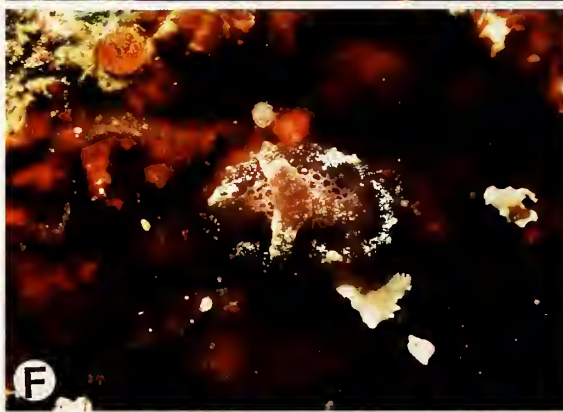
lows: AM, Australian Museum, Sydney; BPBM, Bernice P. Bishop Museum, Honolulu; CASIZ, California Academy of Sciences, San Francisco; SAM, South African Museum, Cape Town; USNM, National Museum of Natural History, Washington.

SPECIES DESCRIPTIONS

Hallaxa Eliot, 1909

Type species: *Halla decorata* Bergh, 1878, by original designation. *Hallaxa* was a replacement name for *Halla* Bergh, 1878, a junior homonym of a genus of polychaete annelid.

Diagnosis: Body fleshy, without spicules, ovoid, elliptical or round. Color variable. Most species cryptic on sponge prey. Rhinophores perfoliate, bulbous or rarely conical. Gills unipinnate, 6–14 in number, retractile. Anterior margin of foot straight or concave. Oral tentacles present or modified to oral pits. Jaws armed with undivided or multifid rodlets. Radula without rachidian row of teeth.



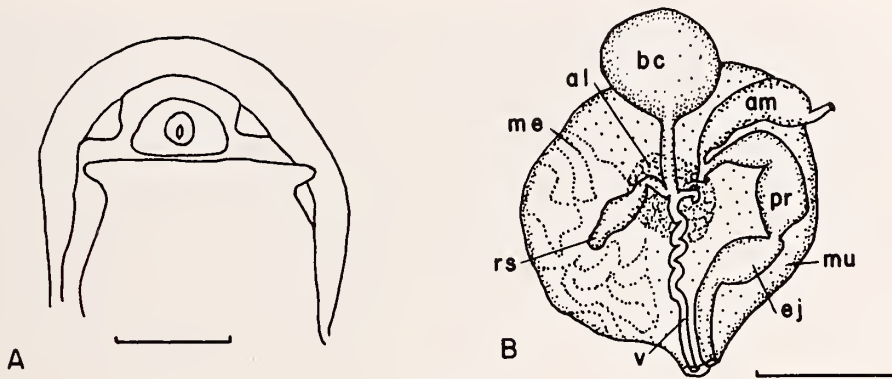


Figure 2

Hallaxa apefae Marcus, 1955. A. Line drawing of ventral view of head, drawn by camera lucida from preserved specimen, scale = 0.5 mm. B. Reproductive system, al- albumen gland, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of the vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 0.5 mm.

Inner lateral teeth broad, denticulate. Outer lateral teeth thin, bearing multiple denticles. Each half row of radula containing 4–22 outer lateral teeth per half row. Reproductive system triaulic. Vas deferens prostatic proximally, ejaculatory more distally. Receptaculum seminis semiserial in arrangement, situated opposite or distal to uterine duct. Membrane gland separate or united with remainder of female gland mass. Penis simple, unarmed.

Hallaxa apefae Marcus, 1957

(Figures 2, 3)

Hallaxa apefae Marcus, 1957:421, figs. 73–80.

Material: One specimen, CASIZ 066166, dissected, Brazil, courtesy of Dr. Eveline Marcus. The specimen was labelled “paratype,” but the original description was based on a single specimen, which was dissected. The present specimen has no formal systematic status, and no locality information was contained with the specimen. It is likely that the specimen was collected from the type locality.

Distribution: This species is known only from the type locality, Ubatuba, Brazil.

External morphology: The living holotype animal described by Er. Marcus (1957) was 7 mm long. It was light yellowish gray with darker viscera showing through the translucent notum. A series of tubercles extended mid-

dorsally from the head to anterior of the branchial plume where they divide and encircle the gills. The present preserved specimen is 7 mm long. Only a trace of the original raised tubercles remains. The body is broad and rounded. The rhinophores have nine lamellae, and there are nine unipinnate gills. The anterior margin of the foot (Figure 2A) is straight with laterally extending anterior foot corners. A pair of triangular lappets is present on the anterior side of the head.

Internal morphology: The labial cuticle consists of numerous rodlets (Figure 3A) with one to four denticles along their free margin. The radular formula was $30 \times 9-11.1.0.1.9-11$ in the holotype and $31 \times 10.1.0.1.10$ in the present specimen. The inner lateral teeth (Figure 3B, C) are broad and thick. The free end of the teeth bears six to seven denticles. The innermost denticle is largest, and they diminish in size outwardly. The outer lateral teeth are narrow and elongate (Figure 3D). The innermost outer lateral tooth bears eight to nine elongate denticles along its inner edge.

The reproductive system (Figure 2B) is triaulic. The pre-ampullary duct is narrow and short. The ampulla is short and wide. It narrows and divides into the short oviduct and the vas deferens. The vas deferens expands into a folded prostatic portion. The prostatic portion narrows to a constriction and again expands into a wide muscular portion that narrows and terminates at the common genital

Figure 1

Living animals. A. *Hallaxa atrotuberculata* Gosliner & Johnson, sp. nov., photo by T.M.G. B. *Hallaxa translucens* Gosliner & Johnson, sp. nov., photo by T.M.G. C. *Hallaxa iju* Gosliner & Johnson, sp. nov., photo by T.M.G. D. *Hallaxa elongata* Gosliner & Johnson, sp. nov., photo by T.M.G. E. *Hallaxa paulinae* Gosliner & Johnson, sp. nov., photo by Pauline Fiene-Severns. F. *Hallaxa hileenae* Gosliner & Johnson, sp. nov., photo by T.M.G. G. *Hallaxa cryptica* Gosliner & Johnson, sp. nov., purple form, photo by T.M.G. H. *Hallaxa michaeli* Gosliner & Johnson, sp. nov., photo by Michael Gosliner.

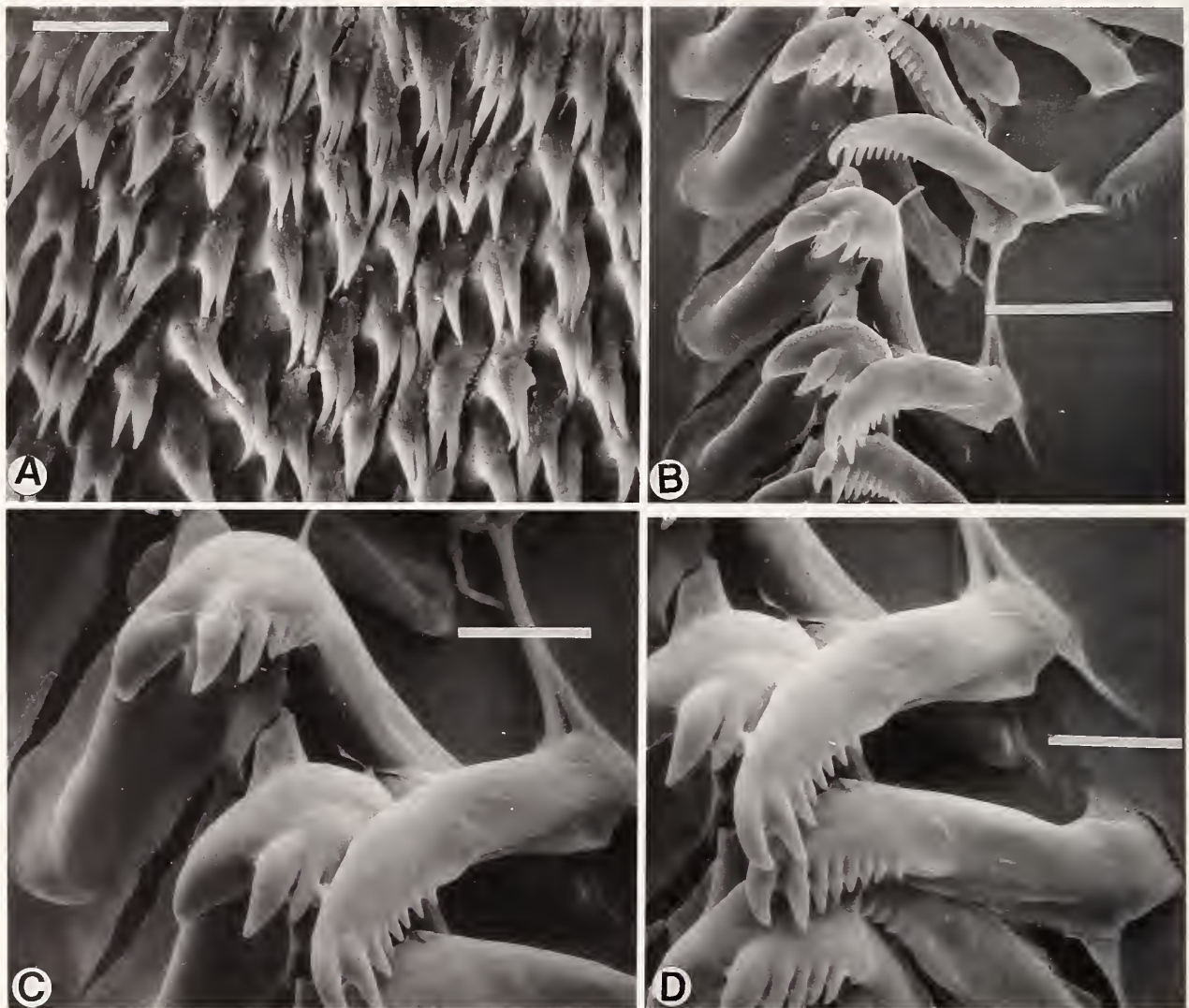


Figure 3

Hallaxa aepfae Marcus, 1955. Scanning electron micrographs. A. Jaw rodlets, scale = 10 μm . B. Inner lateral and adjacent outer lateral teeth, scale = 25 μm . C. Inner lateral teeth, scale = 10 μm . D. Innermost outer lateral teeth, scale = 10 μm .

opening. The vaginal opening is immediately adjacent to the proximal termination of the vas deferens. The vagina is narrow and elongate. It includes several loops and has a common junction with the ducts of the bursa copulatrix, receptaculum seminis, and the uterine duct. The receptaculum seminis is pyriform and elongate. The bursa copulatrix is large and spherical. The female gland mass is composed of three portions, the albumen, membrane, and mucous glands.

Discussion: The specimen examined here is virtually identical to the morphology originally depicted by Er. Marcus (1957). The only significant difference is the absence of a vaginal diverticulum and the more proximal position of

the uterine duct in the present material. The uterine duct is situated at the juncture of the receptaculum seminis with the vagina. As no other species of *Hallaxa* has the vaginal diverticulum, it is doubtful that Marcus actually observed this structure in the holotype.

Hallaxa aepfae is relatively plesiomorphic in its anatomy and can be distinguished from all other species by having a mid-dorsal, longitudinal line of tubercles that divides and encircles the gills.

Hallaxa chani Gosliner & Williams, 1975

(Figures 4, 5)

Hallaxa chani Gosliner & Williams, 1975:396, figs. 2-8.

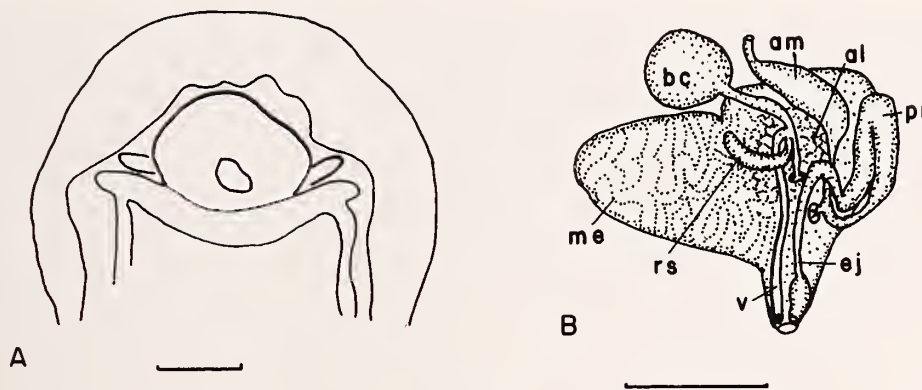


Figure 4

Hallaxa chani Gosliner & Williams, 1975. A. Line drawing of ventral view of head and foot of preserved specimen, drawn with camera lucida, scale = 1.0 mm. B. Reproductive system, al- albumen gland, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, ud- uterine duct, v- vagina, scale = 0.5 mm.

Material: Paratype radula, CASIZ 020376. One specimen, CASIZ 070787, dissected, intertidal, North Shell Beach, San Luis Obispo County, California, 31 December 1971, G. McDonald.

Distribution: This species is known along the Pacific coast of North America from Grant Island, Ketchikan, Alaska to San Luis Obispo County, California (Behrens, 1991).

External morphology: The living animals are translucent yellowish with numerous dermal brown patches showing through the translucent notum. The body is broad and rounded. The notum is covered with scattered rounded tubercles. The rhinophores have 9–10 lamellae. The branchial plume is composed of 12–14 unipinnate gills. The anterior end of the foot (Figure 4A) is fairly straight with elongate extensions of its anterior corners. A short, digitiform tentacle is present on either side of the mouth.

Internal morphology: The labial cuticle is situated within the anterior end of the buccal mass. It is composed of numerous multifid rodlets. The radular formula is $30 \times 13.1.0.1.13$ and $31 \times 14.1.0.1.14$ in two specimens examined. The inner lateral teeth (Figure 5C, D) are broad, but narrower than those of other species studied here. The free margin of the inner laterals bears a single large cusp on its inner side with four to eight smaller denticles on the outer side. The outer laterals are narrow basally and elongate (Figure 5A, B). The innermost outer lateral tooth bears 7–12 triangular denticles along its inner margin.

The reproductive system (Figure 4B) is triaulic. The pre-ampullary duct is short and narrow. It expands into a thick, saccate ampulla that narrows and passes ventrally under the vas deferens, where it bifurcates into the short oviduct and vas deferens. The proximal part of the vas deferens is prostatic and folded into a large loop. The prostatic vas deferens narrows somewhat as it gives rise to the ejaculatory segment. The vas deferens widens at the

penial sac. The penis exits adjacent to the vaginal duct. The vagina is thin and elongate. It joins the curved, pyriform receptaculum seminis. After a short distance, the vagina and receptaculum join the elongate duct of the bursa copulatrix and the shorter uterine duct. The bursa copulatrix is thin-walled and spherical. The membrane gland is larger than the albumen or mucous glands.

Discussion: The present material is virtually identical to that originally described (Gosliner & Williams, 1975). The only differences are that the bursa copulatrix is spherical in the present material rather than nodular, and there is no vestigial rachidian row of radular teeth. The nodular appearance indicates that the bursa is full of spermatozoa. The previously described vestigial rachidian row is a preservational artifact of the folding of the radular membrane. We reexamined the paratype radula, CASIZ 020376 (formerly 490). No trace of such a row was found in it or any of the present material.

Hallaxa chani is plesiomorphic in all features described, except that the labial rodlets are multifid. It is the only yellowish species with many scattered tubercles.

Hallaxa atrotuberculata

Gosliner & Johnson, sp. nov.

(Figures 1A, 6, 7)

Type material: Holotype: CASIZ 066167, Nosy Komba, Madagascar, 1 m depth, 16 April 1989, T. M. Gosliner. Paratypes: One specimen, BPBM 9943, lagoonside, Enewetak Island (11°21'43"N, 162°21'8"E, Enewetak Atoll, Marshall Islands, 5 m depth, 7 February 1983, S. Johnson. One specimen, BPBM 9944, lagoonside, Enewetak Island, Enewetak Atoll, Marshall Islands, 5 m depth, 7 February 1983, S. Johnson. Two specimens, CASIZ 066168, one dissected, Nosy Tanikely, Madagascar, 2 m depth, 14 April 1989, T. M. Gosliner. One specimen, CASIZ 066169, n.

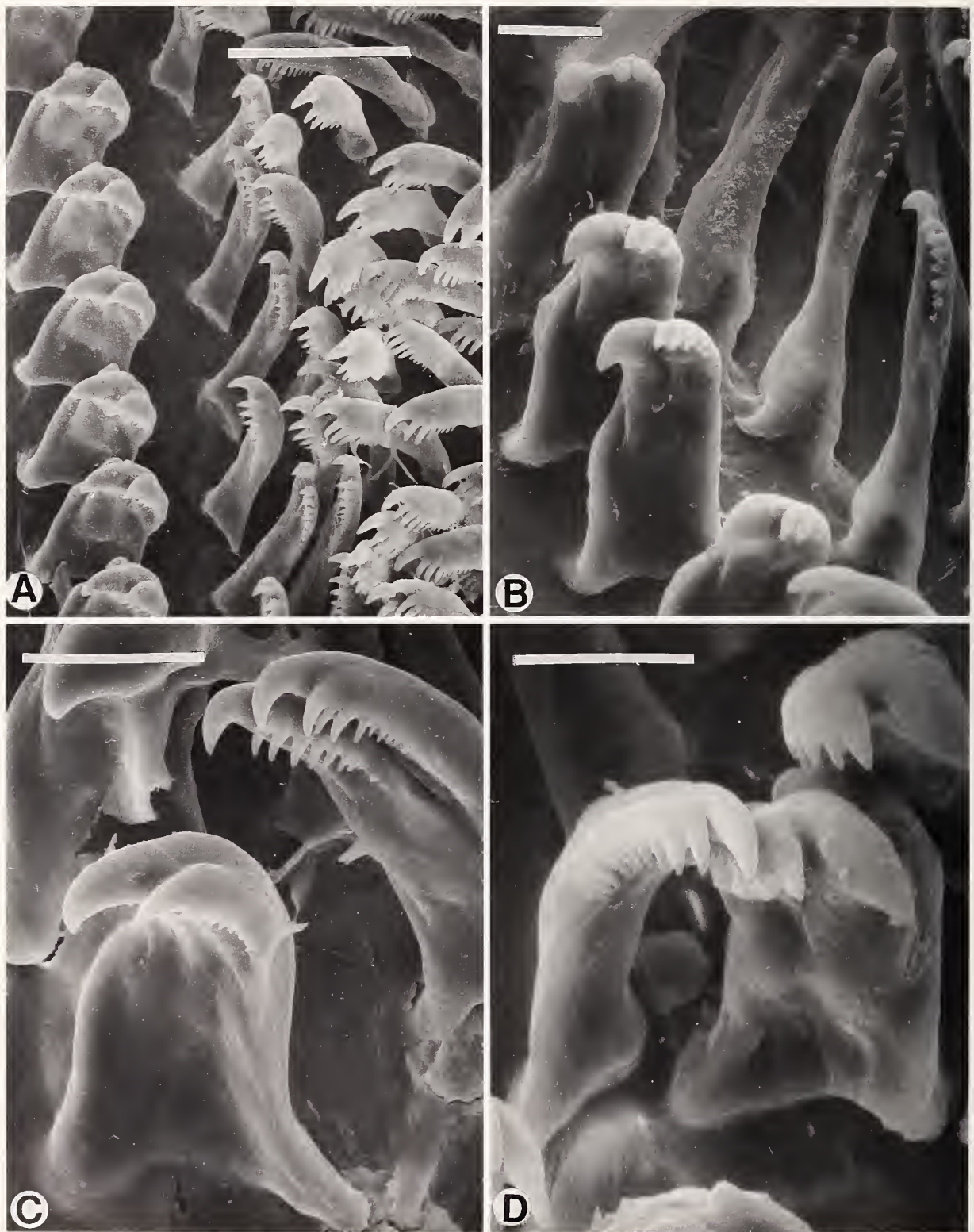


Figure 5

Hallaxa chani Gosliner & Williams, 1975. Scanning electron micrographs of CASIZ 070787. A.-D. Inner and outer lateral teeth, A. scale = 43 μm . B. scale = 20 μm . C. scale = 20 μm . D. scale = 10 μm .

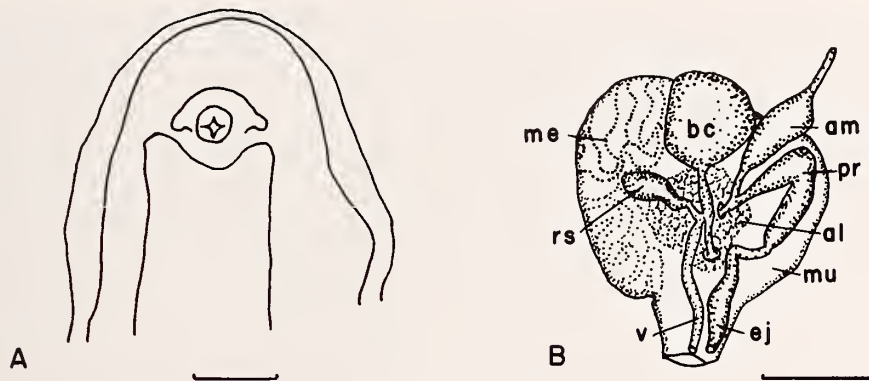


Figure 6

Hallaxa atrotuberculata Gosliner & Johnson, sp. nov. A. Camera lucida line drawing of ventral view of head and foot of preserved specimen, scale = 1.0 mm. B. Reproductive system, al- albumen gland, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 1.0 mm.

side of Andilana Beach, Nosy Be, Madagascar, 15 April 1989, T. M. Gosliner. One specimen, CASIZ 074196, 0.5 km s. of Mahé Beach Hotel, Mahé Island, Republic of the Seychelles, 1 m depth, 2 April 1986.

Distribution: This species has been recorded from the western Indian Ocean from Madagascar and the granitic Seychelles, and from Enewetak Atoll in the western Pacific (present study).

Etymology: The epithet *atrotuberculata* refers to the black tubercles that characterize this species.

External morphology: The living animals (Figure 1A) are 3–18 mm in length. The body is elongate and ovoid. The general body color is light charcoal gray with uniformly scattered black tubercles. The apical portion of the rhinophores is opaque white, while the remainder is black. The gills are uniformly black with an occasional silvery area of pigment located in the center of the plume in the area around the anus of some specimens. The rhinophores are bulbous with 12–14 transverse lamellae. The branchial plume consists of 11–14 unipinnate gills. The anterior end of the foot (Figure 6A) is curved anteriorly, without elongate lateral extensions. A short oral tentacle is present on either side of the mouth.

Internal morphology: The muscular portion of the buccal mass is short relative to the anterior glandular segment. Within the anterior end of the muscular portion of the buccal mass is the labial cuticle. The labial cuticle is composed of several rows of elongate, undivided rodlets (Figure 7A). The radular formula is $27 \times 16.1.0.1.16$, $31 \times 17.1.0.1.17$ (Figure 7B), $33 \times 22.1.0.1.22$ in three specimens examined. The inner lateral teeth are broad and thick with a single primary cusp (Figure 7C, D). On the outer edge of the cusp are one to three small, short denticles. The outer lateral teeth are narrow and elongate (Figure

7E). The innermost outer laterals bear seven to eight elongate denticles. Some of the outer laterals may have as many as 10 denticles along their inner edge. The outermost teeth have only four to five denticles along their margin.

The trialectic reproductive system (Figure 6B) is fully mature. The pre-ampullary duct is narrow and elongate. The ampulla is short and wide. It narrows and divides into the short oviduct and the vas deferens. The vas deferens expands into a folded prostatic portion. The prostatic portion narrows into a thin, curved muscular portion that widens and terminates at the common genital opening. The vaginal opening is immediately adjacent to the distal termination of the vas deferens. The vagina is curved, narrow and elongate. There is a common junction of the vagina with the ducts of the bursa copulatrix and receptaculum seminis, and the uterine duct. The receptaculum seminis is pyriform and elongate. The bursa copulatrix is large and spherical. The female gland mass is composed of three portions—the albumen, membrane, and mucous glands. The membrane gland is not distinctly separated from the albumen and mucous glands.

Discussion: *Hallaxa atrotuberculata* is the only species of *Hallaxa* with large, uniformly scattered tubercles and a black ground color. It also is unique in having an inner lateral tooth with a single broad cusp with minute outer denticles. Also, *H. atrotuberculata* has more outer lateral teeth per half row than any other described species of *Hallaxa*. Its general appearance is reminiscent of species of the closely allied genus *Actinocyclus*. It still retains many primitive features: numerous gills, undivided jaw rodlets, a broad radula, and a thick primary cusp of the inner lateral tooth with secondary denticles. It represents the least derived member of the genus *Hallaxa*. Though it retains some of the primitive features found in species of *Actinocyclus*, it clearly shares several derived features with

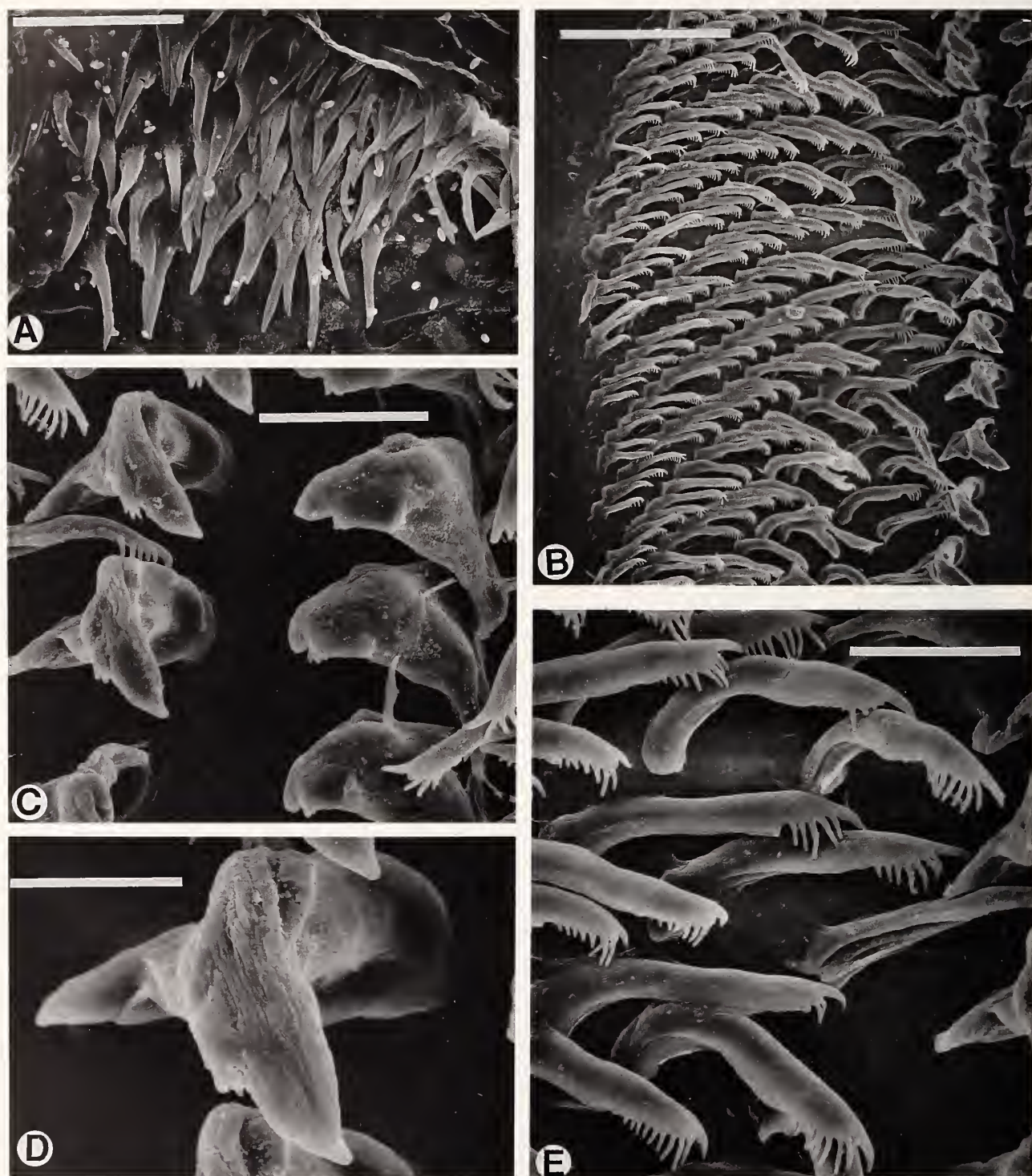


Figure 7

Hallaxa atrotuberculata Gosliner & Johnson, sp. nov. Scanning electron micrographs, CASIZ 066168. A. Jaw rodlets, scale = 20 μm . B. Half row of radular teeth, scale = 100 μm . C. Inner lateral teeth, scale = 30 μm . D. Inner lateral teeth, scale = 15 μm . E. Outer lateral teeth, scale = 30 μm .



Figure 8

Hallaxa translucens Gosliner & Johnson, sp. nov. Living holotype with egg mass on prey sponge.

other species placed in *Hallaxa* (see systematic relationships).

Hallaxa translucens

Gosliner & Johnson, sp. nov.

(Figures 1B, 8–10)

Type material: Holotype: CASIZ 088079, dissected, 6 m depth, Devil's Point, w. side Maricaban Island, off Luzon Island, Philippines, 23 March 1993, T. M. Gosliner.

Distribution: This species is known only from the holotype collected off the southern coast of Luzon Island in the Philippines.

Etymology: The name *translucens* comes from the translucent appearance of the living animal.

External morphology: The living animal (Figure 1B, 8) was 20 mm in length. The body is broad and rounded with a smooth notum. The animal is translucent whitish with a dense network of opaque white pigment. The gills are translucent white, and the rhinophores are uniformly light brown.

The branchial plume consists of 12 unipinnate gills. The rhinophores are bulbous with eight simple lamellae. The anterior end of the foot (Figure 9A) is curved and contains anteriorly directed folds. A short, digitiform oral tentacle is present on either side of the mouth.

Internal morphology: The buccal mass is short and muscular, with a short anterior glandular portion. Near the anterior limit of the muscular portion of the buccal mass is the labial cuticle. The cuticle contains numerous rows of undivided and bifid rodlets (Figure 10A). The radular formula of the single specimen is $40 \times 13.1.0.1.13$ (Figure 10B). The inner lateral teeth (Figure 10C) are relatively narrow basally with a bifid cusp that bears two hook-shaped denticles. No secondary denticles are present on the outer edge of the tooth. The outer lateral teeth (Figure 10D) are thin and elongate. The primary denticle is slightly curved and much longer than the lower denticles. There are 7–11 denticles along the margin of the laterals. The teeth of the innermost outer lateral teeth are more congested and less distinct than those of the outermost teeth. The outermost laterals are as long as the inner ones.

The reproductive system (Figure 9B) is triaulic. The pre-ampullary duct is short and narrow. It expands into

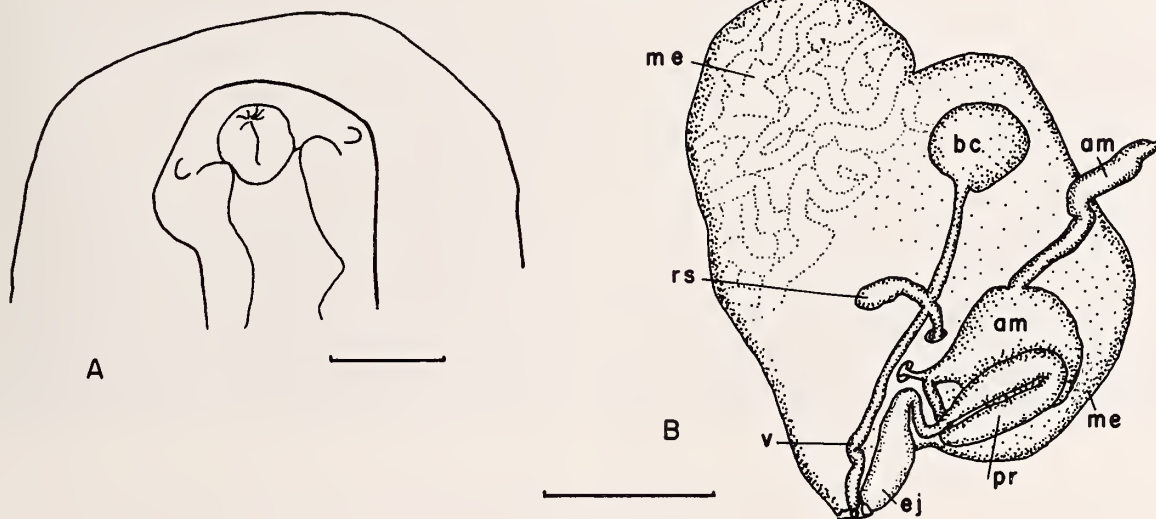


Figure 9

Hallaxa translucens Gosliner & Johnson, sp. nov. A. Camera lucida line drawing of ventral view of head and foot of preserved holotype, scale = 1.0 mm. B. Reproductive system, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 1.0 mm.

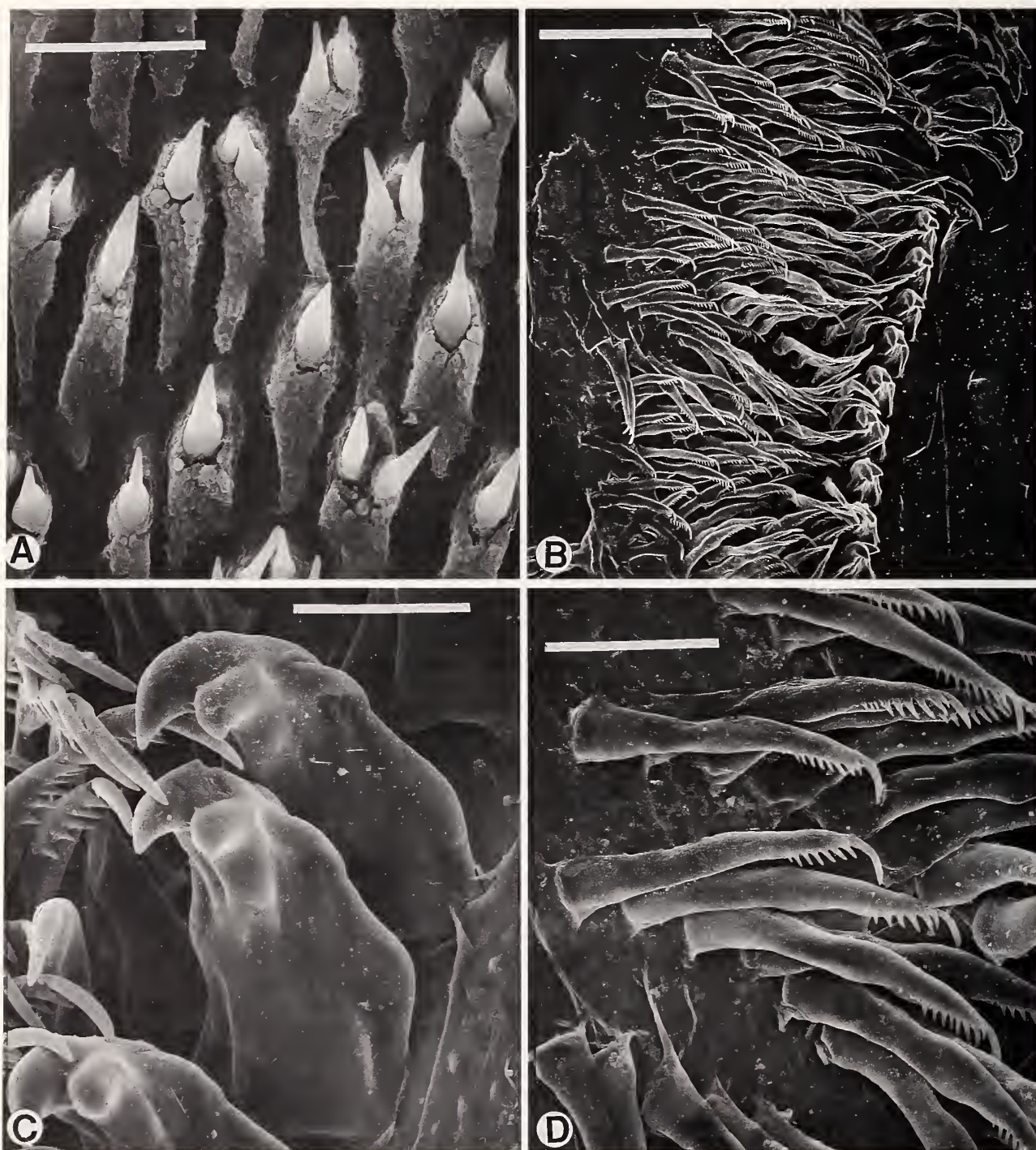


Figure 10

Hallaxa translucens Gosliner & Johnson, sp. nov. Scanning electron micrographs. A. Jaw rodlets of holotype, scale = 10 μm . B. Half row of radular teeth, holotype, scale = 150 μm . C. Inner lateral teeth, holotype, scale = 30 μm . D. Outer lateral teeth, holotype, scale = 43 μm .

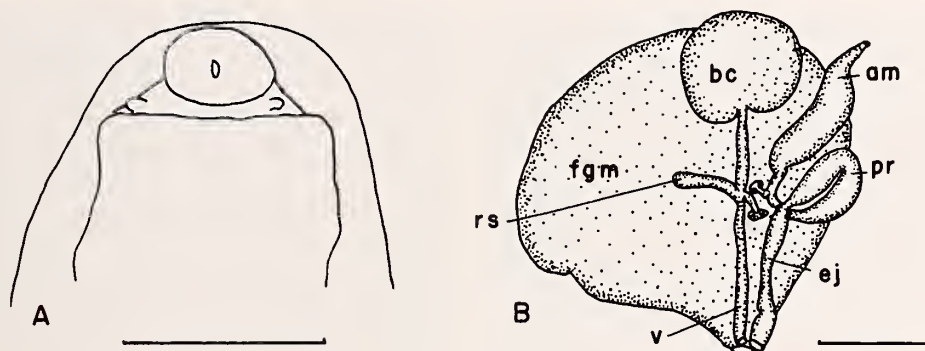


Figure 11

Hallaxa sp. A. Camera lucida line drawing of ventral view of head of preserved specimen, scale = 1.0 mm. B. Reproductive system, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, fgm- female gland mass, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 0.5 mm.

a wide, bulbous ampulla. From the ampulla, the narrow, short postampullary duct divides into the short oviduct, which enters the female gland mass, and the vas deferens. The vas deferens expands into a proximal prostatic portion, which recurves back upon itself and narrows into a short segment. From this narrow portion, the duct again widens into a thick ejaculatory penis that is devoid of armature and exits adjacent to the vagina. The vagina is thin and slightly convoluted. The duct of the pyriform receptaculum seminis is short and enters the vagina opposite the uterine duct. The proximal portion of the vagina is thin and elongate and terminates at the stalked, spherical, thin-walled bursa copulatrix. The membrane gland is somewhat separate from the albumen and mucous glands, but not markedly as in some other species.

Discussion: *Hallaxa translucens* externally resembles other species of *Hallaxa* with white body color. It most closely resembles *H. paulinae* and white specimens of *H. cryptica*. There are several differences in the external morphology of these three species. *Hallaxa translucens* has distinct oral tentacles that are absent in *H. cryptica* and *H. paulinae*. *Hallaxa translucens* and *H. paulinae* both are translucent white with an overlying network of opaque white. However, *H. translucens* has brown bulbous rhinophores, while *H. paulinae* has white conical rhinophores with a black subapical spot and few lamellae. Also the opaque white lines are more crowded in *H. translucens*. Internally, there are other differences. In *H. translucens*, the inner lateral tooth lacks the secondary denticles that are present in *H. paulinae*. There are also other differences in the number and shape of the outer lateral teeth. *Hallaxa translucens* has 13 outer lateral teeth per side, while the same-sized specimens of *H. paulinae* have a maximum of six rows of outer laterals. In *H. translucens*, the outer laterals bear 7–11 elongate, crowded denticles. All of the outer lateral teeth are similar in size and shape. In *H. paulinae*, there are zero to seven denticles on the outer lateral teeth. Their denticles are coarser than in *H. translucens*. The outermost

teeth of *H. paulinae* are smaller than the inner outer laterals, and the outermost teeth lack denticles. Also, in *H. translucens*, the vaginal duct between the gonopore and the duct of the receptaculum seminis is elongate, while it is extremely short in *H. paulinae*. The duct of the receptaculum is short in *H. translucens* and elongate in *H. paulinae*.

Hallaxa cryptica lacks the opaque white network of lines present in both *H. translucens* and *H. cryptica*, but has opaque white spots that resemble tubercles. *Hallaxa translucens* has 12 gills compared to eight in *H. cryptica* and has a shorter, curved, and wide ejaculatory portion of the vas deferens.

Hallaxa sp.

(Figures 11, 12)

Material: Two specimens, National Museum of Natural History USNM 577348, Ang Hin Choburi, Thailand, 3 August 1958, George Moore.

External morphology: The two preserved specimens are 7 and 8 mm in length. The body is elongate and ovoid. The branchial plume consists of 11 unipinnate gills. The bulbous rhinophores have six to seven lamellae. The ventral surface of the foot (Figure 11A) is straight, but lacks elongate extensions of the anterior corners. A short tentacle is present on either side of the mouth.

Internal morphology: The buccal mass is short and muscular. At its anterior end is a thin band of undivided jaw rodlets (Figure 12A). There are only three to four rows of rodlets along the region that contains rodlets. The radular formula is $30 \times 6-7.1.0.1.6-7$ in one specimen where the radula is complete. The inner lateral teeth (Figure 12B, C) are only slightly wider than the outer laterals. They have a sharp triangular cusp, with three to four elongate denticles on the outer side of the teeth. The outer lateral teeth (Figure 12D) have four to seven elongate

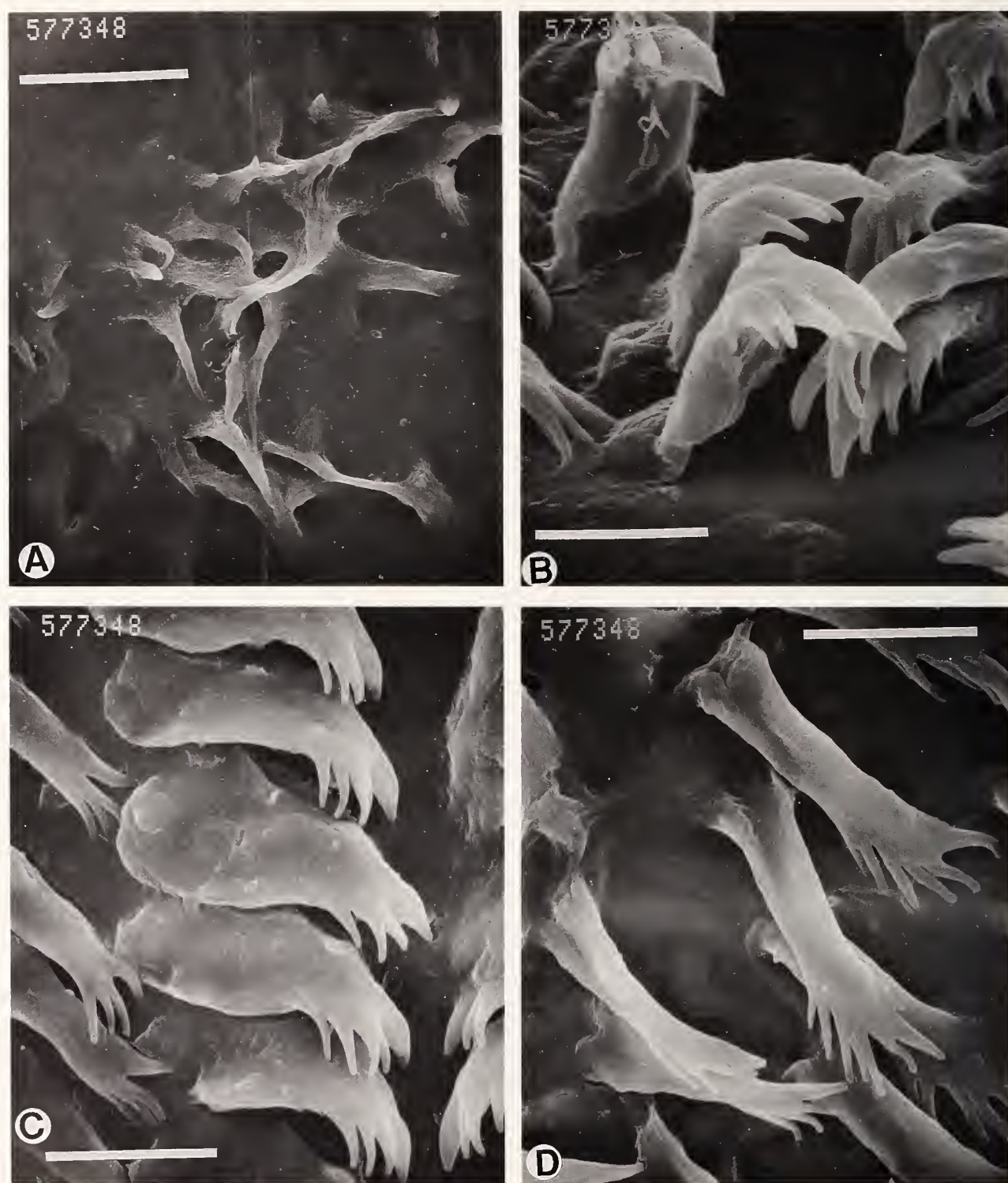


Figure 12

Hallaxa sp. Scanning electron micrographs, USNM 577348. A. Jaw rodlets, scale = 15 μm . B.-C. Inner lateral teeth, B. scale = 7.5 μm , C. scale = 10 μm . D. Outer lateral teeth, scale = 10 μm .

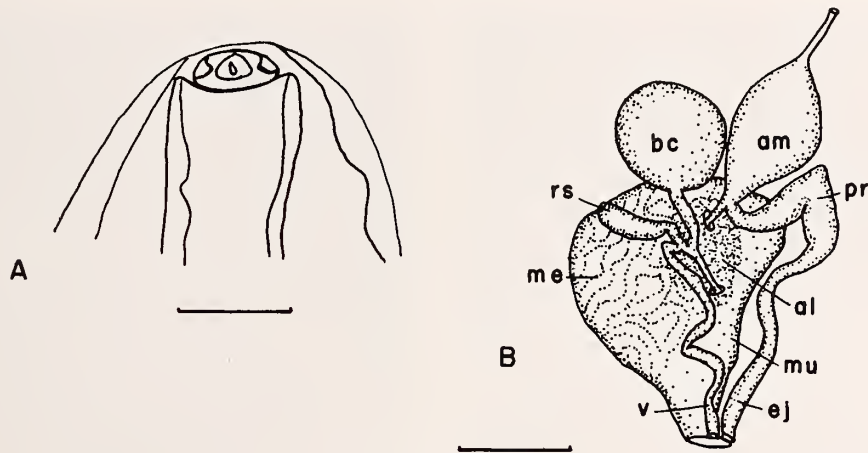


Figure 13

Hallaxa iju Gosliner & Johnson, sp. nov. A. Camera lucida line drawing of ventral view of head of preserved specimen, scale = 1.0 mm. B. Reproductive system, al- albumen gland, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 0.75 mm.

denticles along their surface. Some of the outermost teeth lack denticles entirely.

The reproductive system (Figure 11B) is triaulytic. The pre-ampullary duct is thin and short, and expands into the ampulla. The ampulla again narrows and divides into the short oviduct and the vas deferens. The proximal part of the vas deferens is prostatic. It loops distally and narrows into the ejaculatory portion, which terminates at the common gonopore adjacent to the vagina. The vagina is thin, straight, and elongate. A short, digitiform receptaculum seminis joins the vagina immediately opposite the short uterine duct. The vagina continues proximally, and joins the large, spherical bursa copulatrix. The female gland mass consists of large membrane and mucous glands, and a smaller albumen gland. The membrane gland is continuous with the lobes of the other glands.

Discussion: *Hallaxa* sp. is similar in appearance to *H. decorata*, which is known only from its original, incomplete description. *Hallaxa decorata* differs from the present species in having a stronger cusp on the inner lateral tooth, with more, shorter denticles. It also has more outer lateral teeth per row, and they are more regularly arched in shape, as compared to the more fimbriate denticulation of the present material. The present material has radular teeth that are similar in form to *H. gilva*, but again has fewer teeth per half row. It also differs from *H. gilva*, and all other species of *Hallaxa*, in having a reduced area of jaw rodlets. The labial rodlets of *H. sp.* are undivided rather than multifid, as in *H. gilva*. Most other species have at least 10 rows of rodlets. It would appear that the present material represents an undescribed species. Since the appearance of the living animal remains unknown, we have decided not to describe this species at present.

Hallaxa iju Gosliner & Johnson, sp. nov.

(Figures 1C, 13, 14)

Type material: Holotype, California Academy of Sciences, CASIZ 069937, Barracuda Point, e. side of Pig Island, Madang Lagoon, Madang Province, Papua New Guinea, 9 m depth, 27 August 1989, E. Sobeck. Paratypes: One specimen, BPBM 9945, under dead coral, Reefer 8 Pinnacle, Enewetak Atoll, Marshall Islands, 15 m depth, 6 September 1981, S. Johnson. One specimen, BPBM 9946, lagoonside, Enewetak Island, Enewetak Atoll, Marshall Islands, under dead coral head, 3 m depth, 19 September 1981, S. Johnson. One specimen, CASIZ 079271, dissected, Horseshoe Cliffs, 1 km wnw. of Onna Village, Okinawa, Ryukyu Islands, 3 m depth, 18 July 1991, R. F. Bolland. One specimen, CASIZ 075835, outer barrier reef, s. of Wongat Island, Madang Lagoon, Papua New Guinea, 24 November 1990, T. M. Gosliner. One specimen, CASIZ 083755, Layaglayag, n. side of Maricaban Island, off s. end of Luzon Island, Philippine Islands, 9 m depth, 24 February 1992, T. M. Gosliner.

Distribution: This species has been found at several localities in the western Pacific, from the Marshall Islands, Papua New Guinea, Okinawa, and the Philippines.

Etymology: The specific name is the Marshallese word for star, which refers to the stellate appearance of the rhinophores when viewed from above.

External morphology: The living animals (Figure 1C) are 6–8 mm in length. The body is elongate, ovoid, largely reddish-brown to black. There are small, scattered opaque white spots situated on small tubercles scattered on the notum and on the basal third of the gills. Opaque white

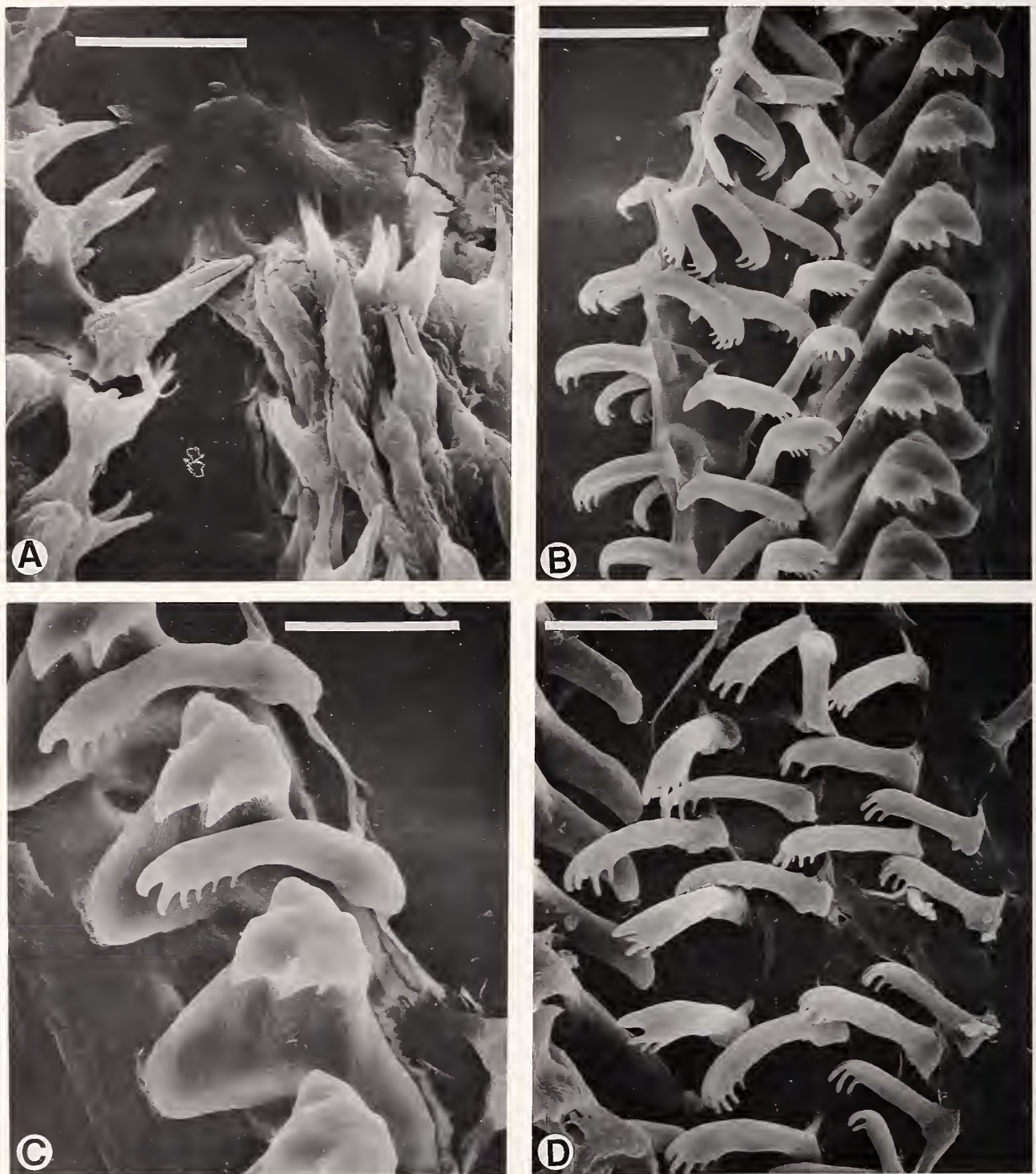


Figure 14

Hallaxa iju Gosliner & Johnson, sp. nov. Scanning electron micrographs. A. Jaw rodlets, Okinawa, CASIZ 079271, scale = 7.5 μ m. B. Half row of radular teeth, Okinawa, CASIZ 079271, scale = 30 μ m. C. Inner lateral teeth, Enewetak, BPBM 9945, scale = 15 μ m. D. Outer lateral teeth, Philippines, CASIZ 083755, scale = 20 μ m.

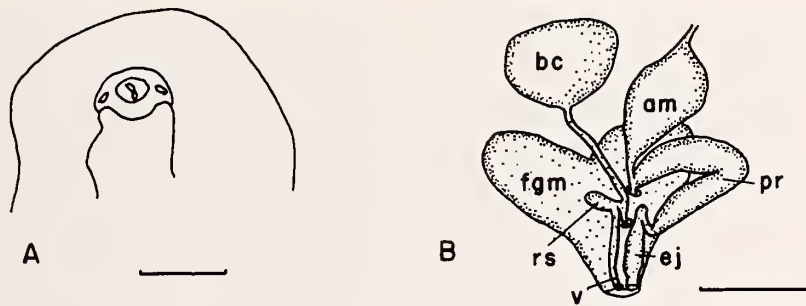


Figure 15

Hallaxa elongata Gosliner & Johnson, sp. nov. A. Camera lucida line drawing of ventral view of head, scale = 1.0 mm. B. Reproductive system, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, fgm- female gland mass, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 0.75 mm.

pigment covers the distal two-thirds of the rhinophoral rachis and lamellae in most specimens. There are five to nine expanded rhinophoral lamellae. The branchial plume consists of 8–10 unipinnate gills. The foot (Figure 13A) is somewhat curved anteriorly, but is straighter than that of most other species. A short, triangular oral tentacle is present on either side of the mouth.

Internal morphology: The buccal mass is short and muscular posteriorly, and elongate and glandular anteriorly. At the anterior end of the muscular portion of the buccal mass is the thin labial cuticle, which bears several rows of rodlets. The rodlets (Figure 14A) are undivided, bifid, or trifold. The radular formula is $14 \times 4.1.0.1.4$, $19 \times 6.1.0.1.6$, $20 \times 8.1.0.1.8$, $22 \times 5.1.0.1.5$ and $26 \times 10.1.0.1.10$ in five specimens examined. The inner lateral teeth (Figure 14B, C) are broad and thick. The free margin bears a bifid cusp with two primary denticles. The outer cusp may have a series of zero to three denticles on the outer side of the cusp. The only specimen that lacked denticles on some teeth was the smallest specimen examined. Some of the inner lateral teeth have one or two denticles on the margin, while others in the same specimen lack denticles entirely (Figure 14C). The outer lateral teeth are narrow basally and elongate. They bear a series of sparse denticles on their inner margin. The innermost outer lateral teeth (Figure 14C) have 4–12 denticles, while the outermost teeth (Figure 14D) have three to five denticles.

The reproductive system (Figure 13B) is triaulic. The pre-ampullary duct is narrow and short. The ampulla is straight and inflated. It narrows and divides into a short oviduct and vas deferens. The vas deferens expands into a folded prostatic portion. The prostatic portion narrows into a muscular portion that is the same diameter through most of its length. It terminates at the common genital opening. The vaginal opening is immediately adjacent to the proximal termination of the vas deferens. The vagina is narrow and elongate. It includes several loops and joins the ducts of the receptaculum seminis. After a short distance, these combined ducts join with the duct of the bursa copulatrix and the uterine duct. The receptaculum seminis

is pyriform and elongate. The bursa copulatrix is large and spherical. The female gland mass is composed of three portions, the albumen, membrane, and mucous glands, which are not well-separated from each other.

Discussion: *Hallaxa iju* can be immediately distinguished from all other members of the genus by the expanded margins of the rhinophoral lamellae. The radula, with multiple denticles along the margin of the inner lateral tooth, is similar to that described for six other species of *Hallaxa*. Of these, only *H. atrotuberculata* and *H. iju* are darkly pigmented. In contrast to *H. atrotuberculata*, *H. iju* lacks distinct tubercles and has a smooth notum and a much narrower radula.

Hallaxa elongata Gosliner & Johnson, sp. nov.

(Figures 1D, 15, 16)

Type material: Holotype: CASIZ 074119, between Passe Femme and Passe du Bois, Aldabra Atoll, Republic of the Seychelles, intertidal, 21 March 1986, B. F. Kensley. Paratypes: Two specimens, California Academy of Sciences, CASIZ 074153, between Passe Femme and Passe du Bois, Aldabra Atoll, in coral rubble, intertidal, 21 March 1986, T. M. Gosliner. One specimen, CASIZ 074259, between Passe Femme and Passe du Bois, Aldabra Atoll, intertidal, 21 March 1986, B. F. Kensley. Four specimens, CASIZ 074249, two dissected, same locality as above, intertidal 19 March 1986, T. M. Gosliner. One specimen, CASIZ 074162, same locality and date as above. Two specimens, CASIZ 074256, same locality and date as above.

Distribution: This species is presently known only from Aldabra Atoll, in the western Indian Ocean, where it is found intertidally in coralline algal rubble.

Etymology: The specific name *elongata* comes from the relatively thin, elongate body, when compared to other members of the genus.

External morphology: The living animals (Figure 1C) are 5–12 mm in length and elongate, elliptical in shape.

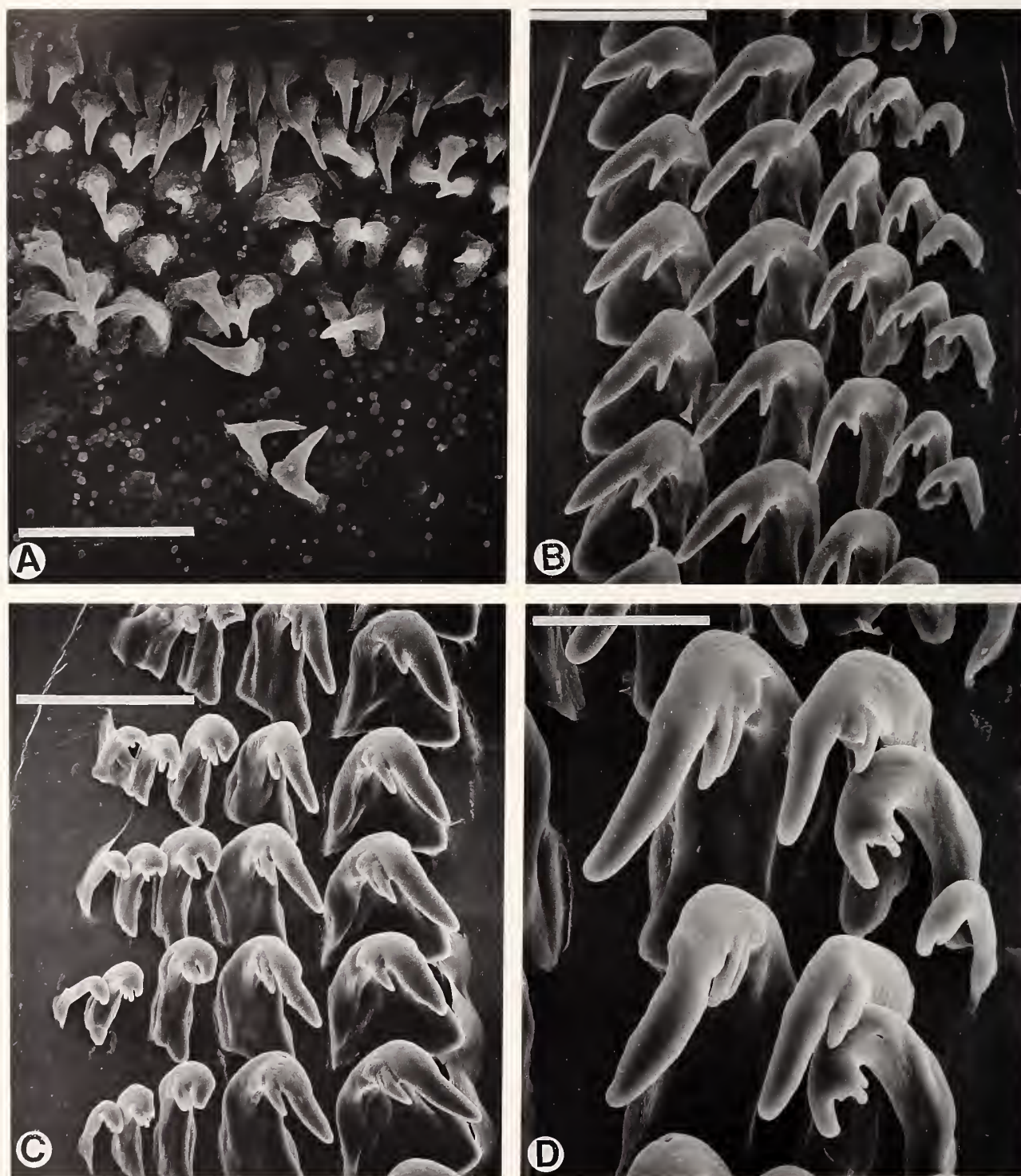


Figure 16

Hallaxa elongata Gosliner & Johnson, sp. nov. CASIZ 074249. A. Jaw rodlets, scale = 25 μ m. B. Half row of radular teeth, scale = 43 μ m. C. Half row of radular teeth, scale = 60 μ m. D. Outer lateral teeth, scale = 25 μ m.



Figure 17

Hallaxa albopunctata Gosliner & Johnson, sp. nov. Living animal.

The animal is uniformly lime green in color with scattered opaque white spots on the tips of minute, scattered tubercles. The apical third of the rhinophores is covered with opaque white, while the basal two-thirds is green. The gills are covered with opaque white pigment. The branchial plume is composed of seven to nine unipinnate gills. The rhinophores are bulbous with seven to nine lamellae. The anterolateral margins of the foot (Figure 15A) are anteriorly directed, and the foot is curved. On either side of the mouth is a folded depression, but no oral tentacles are present.

Internal morphology: The buccal mass is muscular posteriorly, with a larger anterior glandular portion. At the anterior end of the muscular portion of the buccal mass is the labial cuticle. The cuticle contains several rows of largely simple, undivided rodlets (Figure 16A), though an occasional bifid rodlet may be present. The radular formula is $25 \times 4.1.0.1.4$ in the two specimens examined. The inner lateral teeth (Figure 16B, C) are broad and thick. They bear an elongate cusp on their inner side. On the outer side are one to two smaller denticles. The succeeding lateral teeth (Figure 16D) are successively narrower, but not as markedly as in other species. The second through fifth laterals also have one or two laterals on the outside of the primary cusp.

The reproductive system (Figure 15B) is triaulic and largely mature in the largest specimen. The pre-ampullary duct is short and expands into a wide, saccate ampulla. The ampulla narrows abruptly and divides into the short oviduct and the vas deferens. The proximal portion of the vas deferens is prostatic and folded. The prostatic portion narrows into a short, straight ejaculatory segment that is highly muscularized. The vas deferens terminates adjacent to the vaginal duct. The vagina is extremely thin and flimsy. This may reflect that, even in the largest specimens

collected, the female reproductive system may not be fully mature. The vagina is straight and joins the duct of the digitiform receptaculum seminis immediately prior to their common junction with the uterine and bursa copulatrix ducts. The bursa is large and spherical with a thin, elongate duct.

Discussion: This species is distinguishable from other members of the genus by its elongate body form. Internally, it differs from other species of *Hallaxa* by its distinctive radular morphology. It is the only species in which the first outer lateral tooth does not differ markedly from the innermost lateral. The outermost teeth are more similar to those found in other members of the genus, but have fewer denticles than other species. There is little doubt that this species is closely allied to other species of *Hallaxa*, despite the radular differences. It shares similar derived reproductive morphology and the unique arrangement of the oral region and foot, complete with glandular pits.

Hallaxa albopunctata Gosliner & Johnson, sp. nov.

(Figure 17–19)

Hallaxa sp. Gosliner, 1987:69, fig. 91.

Type material: Holotype, SAM A35367, radula removed, Vetchies Pier, n. of Durban Harbor, Durban, South Africa, 2 m depth, 28 April 1982, T. M. Gosliner. Paratype, dissected, SAM A38164, same locality and date as holotype.

Distribution: This species has been collected only from the type locality, Durban, Natal, South Africa.

Etymology: The name *albopunctata* refers to the small white punctations found on the notum of this species.

External morphology: The living animals (Figure 17) are 6 mm in length. The general body color is pale translucent yellow. The body is elongate and ovoid in shape. Scattered opaque white spots are present on low, irregular tubercles distributed unevenly around the notum. Brownish pigment is present around the base of the rhinophore club. The rhinophores are bulbous with seven simple lamellae in the two specimens. The branchial plume consists of seven to eight unipinnate gills. The foot (Figure 18A) is curved anteriorly. The anterior foot corners are elongate and anteriorly directed. A small pit is present on either side of the mouth.

Internal morphology: The labial cuticle consists of numerous multifid rodlets. The radular formula is $24 \times 7.1.0.1.7$ in the one specimen with the complete radula. The inner lateral teeth are broad and thick (Figure 19A–C). They bear a single primary cusp on their inner side and three to four smaller denticles on the outer side. The outer lateral teeth are narrow basally, and elongate; and bear five to seven elongate denticles along their inner margin (Figure 19A, B, D).

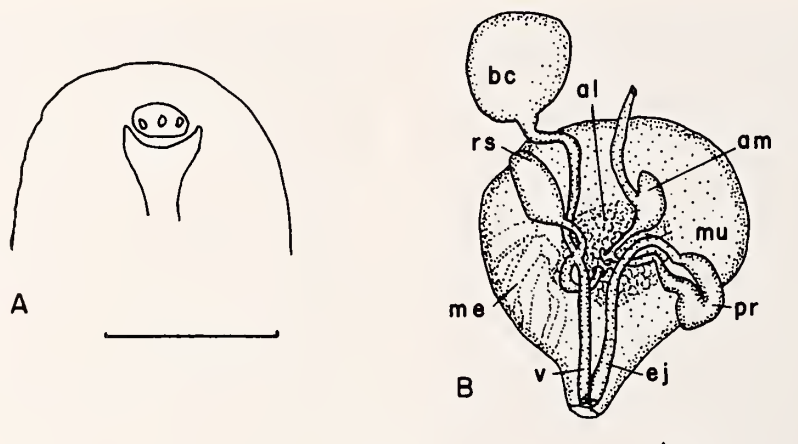


Figure 18

Hallaxa albopunctata Gosliner & Johnson, sp. nov. A. Camera lucida line drawing of ventral view of head and foot of preserved specimen, scale = 1.0 mm. B. Reproductive system, al- albumen gland, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 0.5 mm.

The reproductive system (Figure 18C) is triaulic. The pre-ampullary duct is elongate and thin. It widens into a short, saccate ampulla. The ampulla narrows and bifurcates into the vas deferens and the oviduct. The vas deferens widens into a curved prostatic portion. The duct is constricted in the region where the prostatic portion ends and the ejaculatory portion begins. The ejaculatory portion is elongate and terminates in the penis adjacent to the thin vaginal duct. The vagina is thin and elongate throughout its length. The bursa copulatrix is thin and spherical with a thin, elongate duct. The receptaculum seminis is thick and pyriform, with a short duct. The ducts of the bursa and receptaculum join the vagina in a common junction with the short uterine duct. The mucous gland is much larger than the membrane or albumen glands.

Discussion: *Hallaxa albopunctata* is similar to *H. elongata* and *H. gilva* Miller, 1987, in having a yellowish to greenish body color. However, *H. albopunctata* is unique in having a broad, multicuspid inner lateral tooth. *Hallaxa albopunctata* and *H. elongata* have an oral pit on either side of the mouth, while *H. gilva* retains oral tentacles. *Hallaxa albopunctata* has outer lateral teeth similar to those found in other members of the genus, while those of *H. elongata* are highly modified and more similar to the inner lateral teeth.

Hallaxa paulinae Gosliner & Johnson, sp. nov.

(Figures 1E, 20, 21)

Type material: Holotype, CASIZ 070401, Manado, Sulawesi, Indonesia, 5 m depth, 24 May 1989, P. Fiene-Severns. Paratype, dissected, CASIZ 069938, same locality and date as holotype. This species was found on an unidentified white sponge, on which it was cryptic.

Distribution: This species is thus far known from Indonesia.

Etymology: This species is named for Pauline Fiene-Severns, who found the type material of this species.

External morphology: The preserved specimens were 15 and 20 mm in length. The living animals (Figure 1E) are round in outline, translucent white with numerous, irregular patches forming a network of opaque white on the smooth notum. The gills are uniformly white. The rhinophores are white with a black subapical spot. The smaller specimen (paratype) has a branchial plume consisting of nine unipinnate gills, while the holotype has eight gills. The rhinophores (Figure 20A) are small and conical in shape. They have only four to five lamellae. The foot (Figure 20B) is curved anteriorly. The anterior foot corners are triangular and anteriorly directed. A small pit is present on either side of the mouth in both specimens.

Internal morphology: The muscular portion of the buccal mass is short, while the more anterior, glandular portion is elongate. Within the anterior portion of the muscular portion is the labial cuticle, which contains several rows of rodlets. The rodlets (Figure 21A) consist of one to five denticles along the outer margin. The radular formula is $29 \times 6.1.0.1.6$ in the paratype specimen. The inner lateral teeth (Figure 21B, C) are broad, but somewhat thinner than those of other species examined. The free end of the tooth bears two curved cusps, with one to three auxiliary denticles at the base of the outer cusp. The six outer lateral teeth per half row are narrow and elongate (Figure 21D). The innermost of the outer laterals bear five to seven well-spaced triangular denticles along their inner margin. The succeeding outer laterals have fewer or more reduced denticles. The outermost laterals lack denticles entirely.

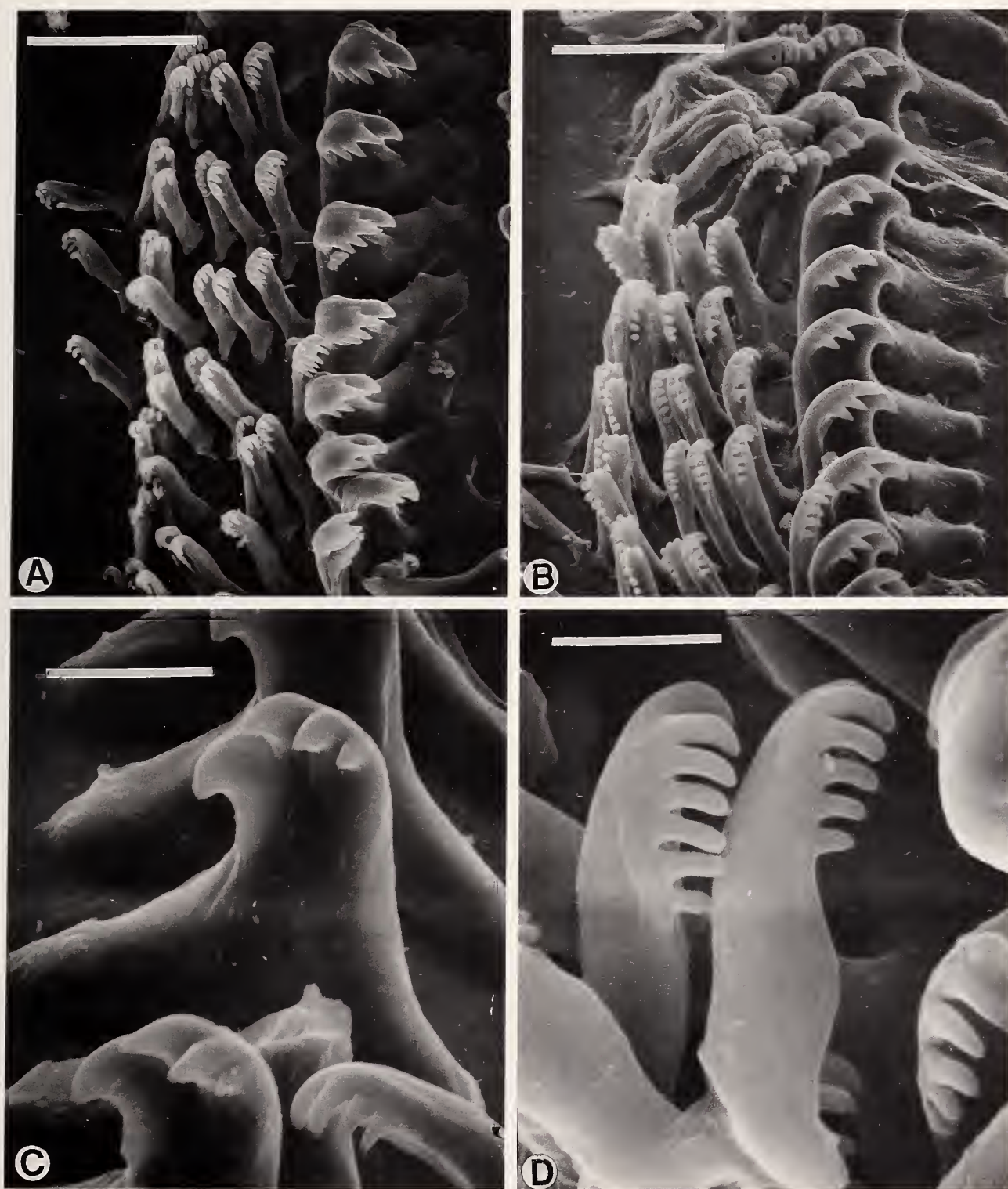


Figure 19

Hallaxa albopunctata Gosliner & Johnson, sp. nov. Scanning electron micrographs, SAM A35367. A. Half row of radular teeth, scale = 30 µm. B. Half row of radular teeth, = 30 µm. C. Half row of radular teeth, scale = 10 µm. D. Outer lateral teeth, scale = 6 µm.

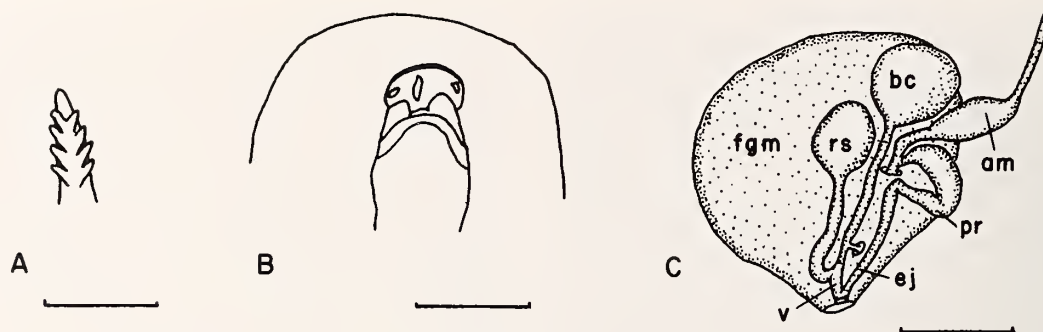


Figure 20

Hallaxa paulinae Gosliner & Johnson, sp. nov. A. Rhinophore, scale = 2.0 mm. B. Camera lucida line drawing of ventral view of head and foot of preserved specimen, scale = 2.0 mm. C. Reproductive system, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, fgm- female gland mass, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 1.0 mm.

The reproductive system (Figure 20C) is triaulic. The pre-ampullary duct is thin and elongate. It expands into the short, saccate ampulla. The ampulla narrows and divides into the short oviduct and the vas deferens. The proximal portion of the vas deferens is prostatic and curved. More distally, the vas deferens narrows into the straight, muscular ejaculatory portion, which terminates at the male gonopore. The distal portion of the vagina is exceedingly short and joins the elongate, curved duct of the relatively large, pyriform receptaculum seminis. After a short distance, these ducts join the short uterine duct and the thin, elongate duct of the bursa copulatrix. The bursa is large and spherical. The glands composing the female gland mass were not well-differentiated in the dissected paratype.

Discussion: Only three species of *Hallaxa* have a whitish body color, *H. paulinae*, *H. translucens*, and the white form of *H. cryptica*; and all of these have a broad foot and are cryptic on sponges. *Hallaxa paulinae* and *H. translucens* have a reticulate pattern on the notum, while *H. cryptica* has large white spots that appear to be tubercles, but are not elevated from the notum. *Hallaxa translucens* and *H. cryptica* also have bidenticulate radular teeth with no auxiliary denticles, while *H. paulinae* has one to three denticles along its outer margin. *Hallaxa paulinae* also has fewer, more sparsely spaced denticles (five to seven) on the outer lateral teeth than do either *H. translucens* (7–11) or *H. cryptica* (7–12). *Hallaxa paulinae* is also unique in having small, conical rhinophores and a short distal vaginal duct.

Hallaxa indecora (Bergh, 1905)

(Figures 22, 23)

Hallaxa indecora Bergh, 1905:116, pl. 15, figs. 3–6.

Hallaxa indecora Bergh, Eliot, 1909:90 (*Halla* Bergh, 1878, preoccupied by *Halla* A. Costa, 1844, a genus of polychaete annelids); Vayssi re, 1912:33, pl. 1, figs. 11–12, pl. 5, figs. 64–70; Baba, 1949:61, fig. 73, pl. 23, fig. 82.

Hallaxa decorata O'Donoghue, 1929:814, fig. 224 (not Bergh, 1878).

Noumea violacea Risbec, 1930:281, figs. 23–30, pl. 1, fig. 5, syn. nov.

Material: One specimen, CASIZ 079357, Horseshoe Cliffs, 1 km wnw. of Onna Village, Okinawa, 3 m depth, 30 May 1991, R. F. Bolland. One specimen, CASIZ 084863, 100 m w. of Waiki-zaki, 5 m depth, 23 July 1991, R. F. Bolland. One specimen, CASIZ 079366, Horseshoe Cliffs, 1 km wnw. Onna Village, Okinawa, Ryukyu Islands, 3 m depth, 23 July 1991, R. F. Bolland.

Distribution: This species is known from Indonesia (Bergh, 1905), the Gulf of Aden (Vayssi re, 1912), Gulf of Suez (O'Donoghue, 1929), New Caledonia (Risbec, 1930), Japan (Baba, 1949), and Okinawa (present study).

External morphology: The living animal is light plum in appearance. Upon closer examination, the notum is translucent white with minute, scattered maroon spots. The body is elongate and ovoid with a smooth notum. The rhinophores and gills are uniformly purplish-brown. The rhinophores are bulbous with seven lamellae. The branchial plume consists of seven unipinnate gills. The foot (Figure 22A) is curved anteriorly, and the anterior foot corners are thin and anteriorly directed. A pit is present on either side of the mouth.

Internal morphology: The buccal mass is short and muscular. The anterior portion is surrounded by a mass of oral glands. Inside the anterior end of the muscular portion of the mass is a circular ring of labial armature. The armature (Figure 23A) consists of a series of rows of irregular rodlets. The radular formula, in the single specimen examined, is $24 \times 8.1.0.1.8$. the inner lateral teeth (Figure 23B, C) are broad and thick. They are curved apically and terminate with a pair of hook-shaped denticles. The two cusps lack any secondary denticles. The outer lateral teeth (Figure 23B, C) are all narrow and elongate,

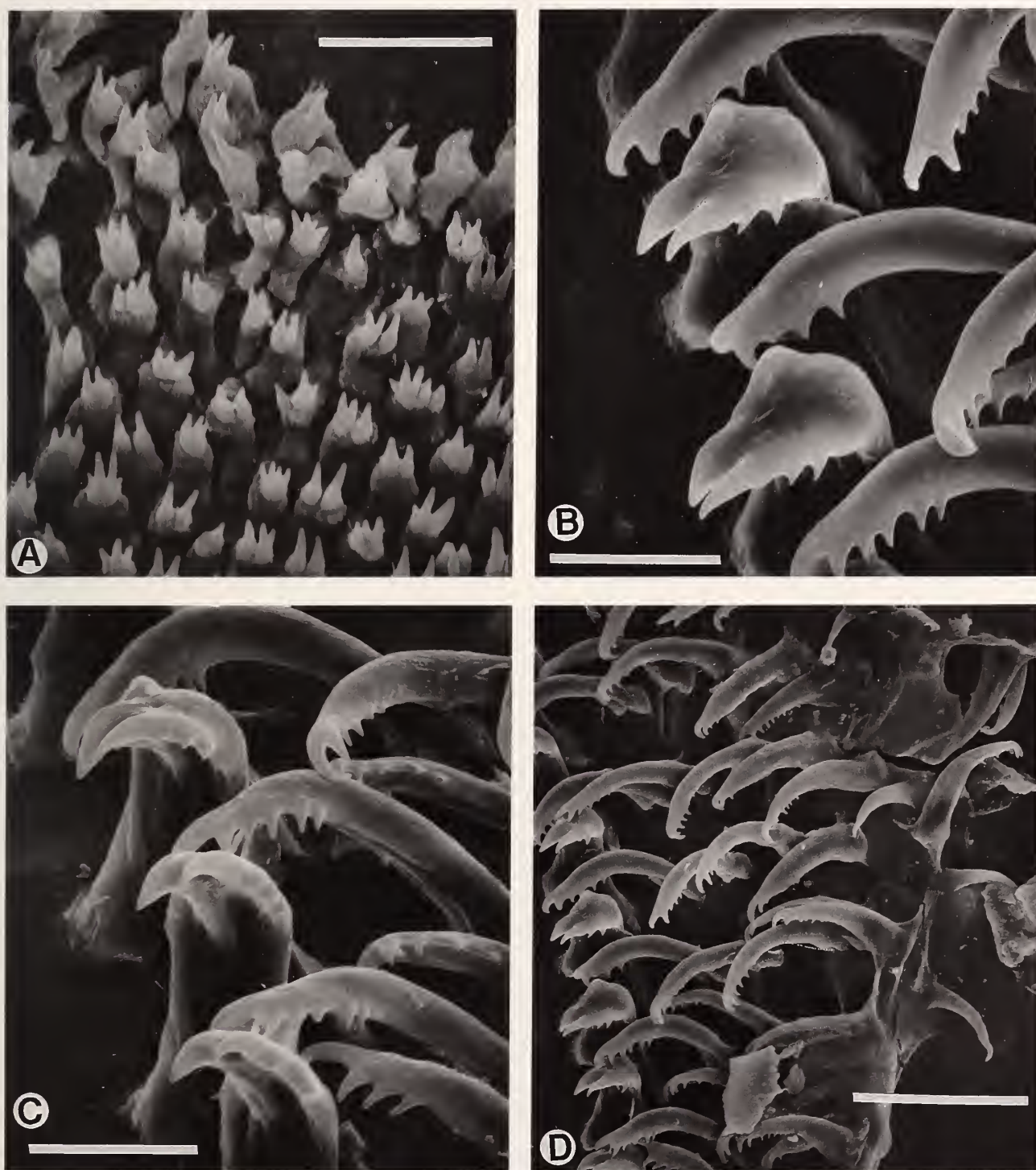


Figure 21

Hallaxa paulinae Gosliner & Johnson, sp. nov., CASIZ 070401. A. Jaw rodlets, scale = 15 μ m. B. Inner lateral teeth, scale = 15 μ m. C. Inner lateral teeth, scale = 15 μ m. D. Outer lateral teeth, scale = 43 μ m.

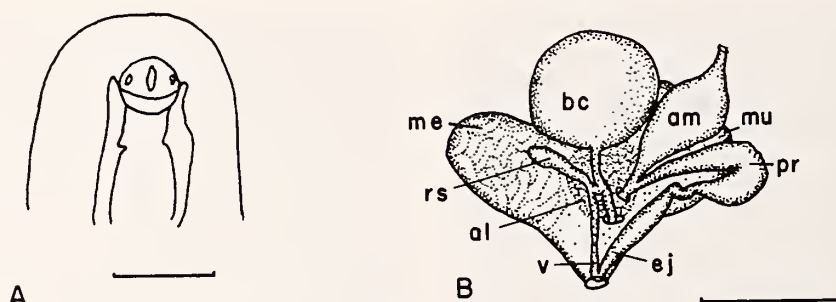


Figure 22

Hallaxa indecora (Bergh, 1905). A. Camera lucida line drawing of ventral view of head and foot of preserved specimen, scale = 0.5 mm. B. Reproductive system, al- albumen gland, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 0.25 mm.

with a series of 12–15 triangular denticles along their inner margin. All of the outer laterals are of similar size and dentition.

The reproductive system (Figure 22B) is triaulic. The narrow pre-ampullary duct expands into a straight, wide ampulla. The ampulla again narrows and divides into the short oviduct and the vas deferens. The proximal part of the vas deferens is wide and prostatic. It curves more distally and narrows into the ejaculatory segment, which terminates at the male gonopore. The vagina is narrow and straight. After a moderate distance, it joins the digitiform receptaculum seminis. After a short distance, the receptaculum duct joins the duct of the bursa copulatrix and the uterine duct. The large bursa is stalked, thin-walled, and spherical. The female gland mass consists of the albumen, membrane, and mucous glands. The membrane gland consists of a discrete lobe largely separate from the other two glands.

Discussion: *Hallaxa indecora* was originally described from nine specimens collected from Aru Island, Indonesia (Bergh, 1905). The radular formula of one specimen described as $60-65 \times 15-20.1.0.1.15-20$. Subsequently, Vayssi re (1912), O'Donoghue (1929, as *H. decorata*), and Baba (1949) recorded specimens from the Gulf of Aden, the Gulf of Suez and Japan. These specimens had radular formulae of $25 \times 6.1.0.1.6$, $33 \times 7.1.0.1.7$, $18-20 \times 8.1.0.1.8$, respectively. The present material from Okinawa is identical in external appearance to that described by Vayssi re, O'Donoghue, and Baba. It agrees in radular formula and shape of teeth. No species of *Hallaxa*, other than Bergh's original description of *H. indecora*, has been described with more than 40 rows of radular teeth (Gosliner & Williams, 1975; Miller, 1987; present study). It is likely that Bergh's count of the radular formula was in error, though the possibility that the material studied by Baba and here may represent a distinct species cannot be eliminated.

Risbec (1930) described *Noumea violacea* based on four specimens collected from New Caledonia. This species is

clearly a *Hallaxa*, based on its bifid inner lateral tooth and elongate, denticulate outer laterals. The color was uniformly wine red in color. It had a radular formula of $20 \times 8.1.0.1.8$. The outer lateral teeth had up to 17 denticles on their margin. All of these features are consistent with the anatomy described for *H. indecora*. On this basis, *Noumea violacea* is here regarded as a junior synonym of *Hallaxa indecora*.

Hallaxa indecora is closely allied to the four other species that have an inner lateral tooth with two large cusps and lack small, auxiliary denticles. The only other species with a purplish color are *H. hileenae* and the purple form of *H. cryptica*. *Hallaxa hileenae* is distinguished from *H. indecora* by having black maculations and a distinct y-shaped ridge on the notum. *Hallaxa indecora* also has more, finer denticles on the outer lateral teeth than does *H. hileenae*. *Hallaxa cryptica* differs in details of coloration, morphology of the anterior foot corners, labial armature, and outer lateral radular tooth denticulation.

Hallaxa hileenae Gosliner & Johnson, sp. nov.

(Figures 1F, 24, 25)

Type material: Holotype, CASIZ 075826, outer barrier reef, between Sek Passage and Wongat Island, Madang Lagoon, Madang, Papua New Guinea, 17 m depth, 25 November 1990, M. Jebb. Paratypes, two specimens partially dissected, CASIZ 086402, s. side Rasch Passage, Madang Lagoon, Madang Province, Papua New Guinea, 6 m depth, 16 June 1992, T. M. Gosliner. Paratype, one specimen, (CASIZ 085971) s. side of lighthouse, 3 km n. of Dakak Resort, near Dapitan City, northern Zamboanga, Mindinao, Philippines, 7 m depth, 31 March 1993, T. M. Gosliner.

Distribution: This species is known from Papua New Guinea, the Philippine Islands, and Guam (Clay Carlson and Patty Jo Hoff, personal communication).

Etymology: This species is named for Eileen Sobeck, who

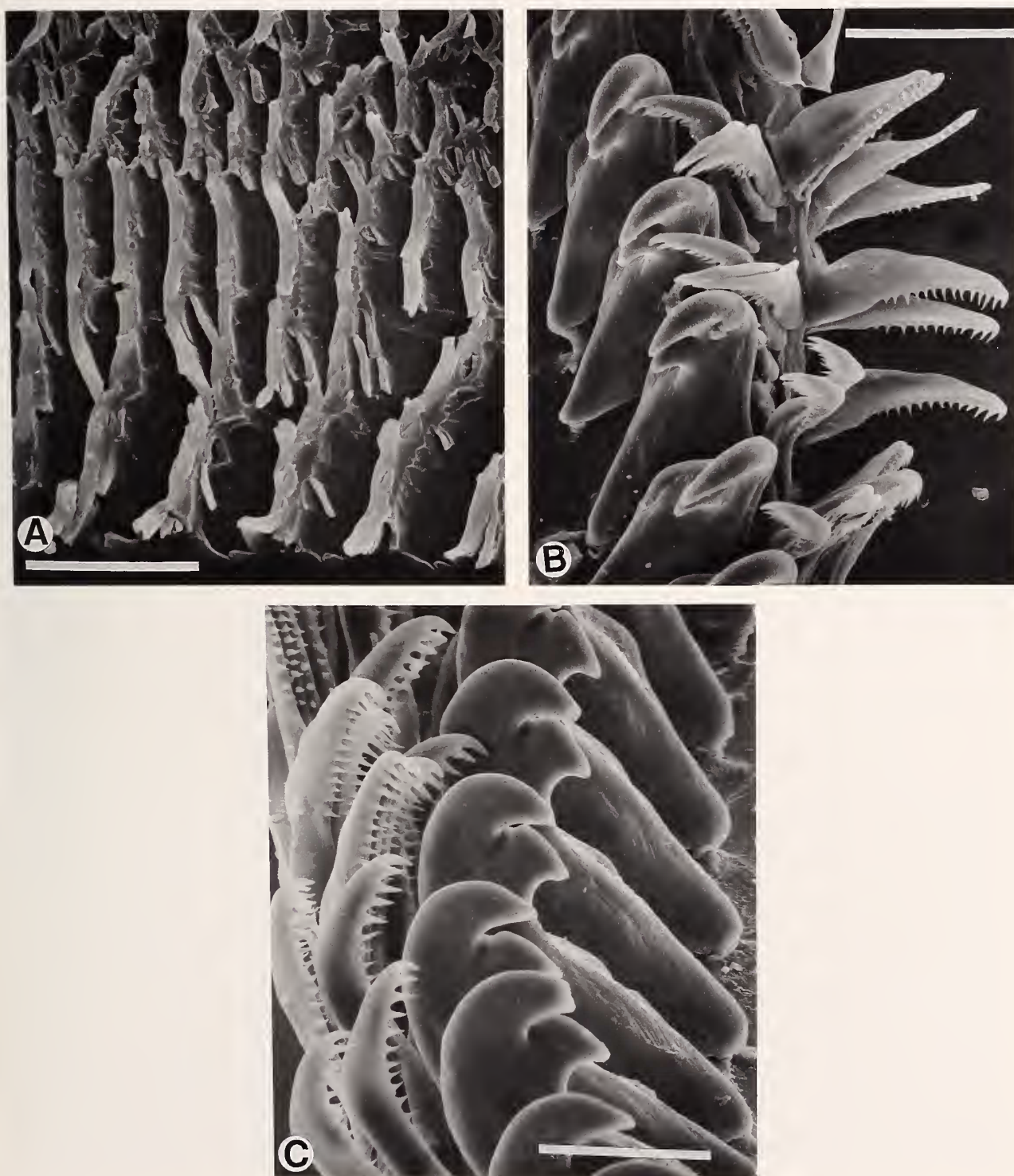


Figure 23

Hallaxa indecora (Bergh, 1905). Scanning electron micrographs, CASIZ 084863. A. Jaw rodlets, scale = 20 μm . B., C. Inner and outer lateral teeth, B. scale = 43 μm , C. scale = 30 μm .

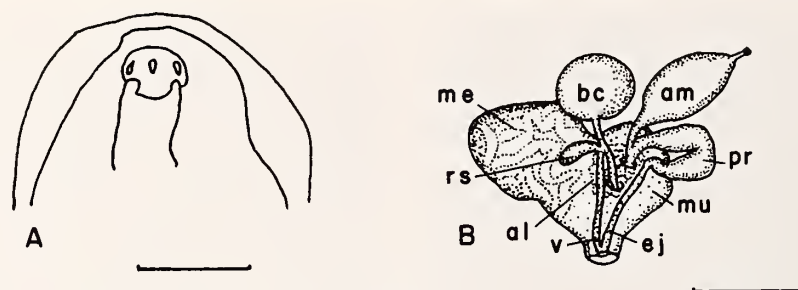


Figure 24

Hallaxa hileenae Gosliner & Johnson, sp. nov. A. Camera lucida line drawing of ventral view of head and foot of preserved specimen, scale = 1.0 mm. B. Reproductive system, al- albumen gland, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 0.5 mm.

assisted in our field work in Papua New Guinea, and collected the first specimen of *Hallaxa iju* from there. Hileen is the Papua New Guinea pidgin name for Eileen.

External morphology: The living animals (Figure 1F) are 5–12 mm in length. The general body color is a wine red. Opaque white pigment is present around the margins of the notum and gills, and on the elevated ridges of the notum. There is also scattered opaque white pigment around the club of the rhinophores, and more densely at their apex. The white pigment is most dense in the outer marginal areas of the notum. The submarginal areas of the notum between the ridges contain irregular charcoal gray to black markings and a few scattered opaque white spots.

The body is elongate and ovoid. A thick longitudinal ridge extends mid-dorsally from the area between the rhinophores and divides into a pair of diagonal ridges, anterior to the gills. Together these ridges form a y-shaped elevated portion of the otherwise smooth notum. The branchial plume consists of six to eight unipinnate gills. The rhinophores are bulbous with five to six lamellae. The foot (Figure 24A) is rounded anteriorly with elongate, anteriorly directed foot corners. A small pit is present on either side of the mouth.

Internal morphology: The buccal mass is short and muscular with a more anterior region of numerous oral glands. The anterior end of the muscular portion contains a ring of labial armature. The labial armature (Figure 25A) contains numerous rows of multifid rodlets, each consisting of three to five denticles. The radular formula is $21 \times 5.1.0.1.5$ and $24 \times 7-8.1.0.1.7-8$ in the two paratypes examined. The inner lateral teeth (Figure 25B, C) are broad and thick with two large, curved cusps on their inner edge. There are no secondary denticles on the inner laterals. The five to eight outer lateral teeth are narrow and elongate, all of similar size and shape (Figure 25C, D). They bear 9–12 elongate denticles. There are slightly fewer denticles on the outermost teeth.

The reproductive system (Figure 24B) is triaulic. The short pre-ampullary duct is narrow and expands into a

saccate ampulla. The ampulla narrows and divides into a short oviduct and the vas deferens. The vas deferens is prostatic proximally. It is curved and narrows distally into a thinner ejaculatory segment. The muscular ejaculatory portion terminates at the gonopore adjacent to the vagina. The vagina is thin and moderately elongate. It joins the small, pyriform receptaculum seminis. Together these ducts connect with the moderately short uterine and bursa copulatrix ducts. The bursa copulatrix is spherical and thin-walled. The uterine duct enters the female gland mass at the albumen gland. The membrane gland is distinct from the remainder of the female gland mass and consists of numerous tubules. The mucous gland is smooth throughout its surface.

Discussion: *Hallaxa hileenae* is immediately distinguishable from other members of the genus by its purple color with black maculations and the distinct y-shaped ridge present on the notum. It is most similar to *H. indecora*, but differs in several external and internal regards (see discussion of *H. indecora*). *Hallaxa hileenae* is a member of the derived subclade of species with bicuspidate inner lateral teeth lacking smaller denticles. Members of this group also have a membrane gland that is a lobe separated from the remainder of the female gland mass.

Hallaxa cryptica Gosliner & Johnson, sp. nov.

(Figures 1G, 26–29)

Type material: Holotype: (white form), CASIZ 085935, Devil's Pt., Maricaban Island, off Batangas Bay, off Luzon Island, Philippines, 3 m depth, 26 March 1993, T. M. Gosliner. Paratypes: One specimen (purple form), Bernice P. Bishop Museum, Honolulu, BPBM 9941, under dead coral head, Ananij Pinnacle ($11^{\circ}28'8''N$, $182^{\circ}22'30''E$), Enewetak Atoll, Marshall Islands, 10 m depth, 10 September 1981, S. Johnson. One specimen (purple form), CASIZ 083764, dissected, Arthur's Rock, Maricaban Peninsula, s. end Luzon Island, Philippine Islands, 15 m depth, 22 February 1992, T. M. Gosliner. One specimen (white form), BPBM 9942, under dead coral head, K-9 Pinnacle,

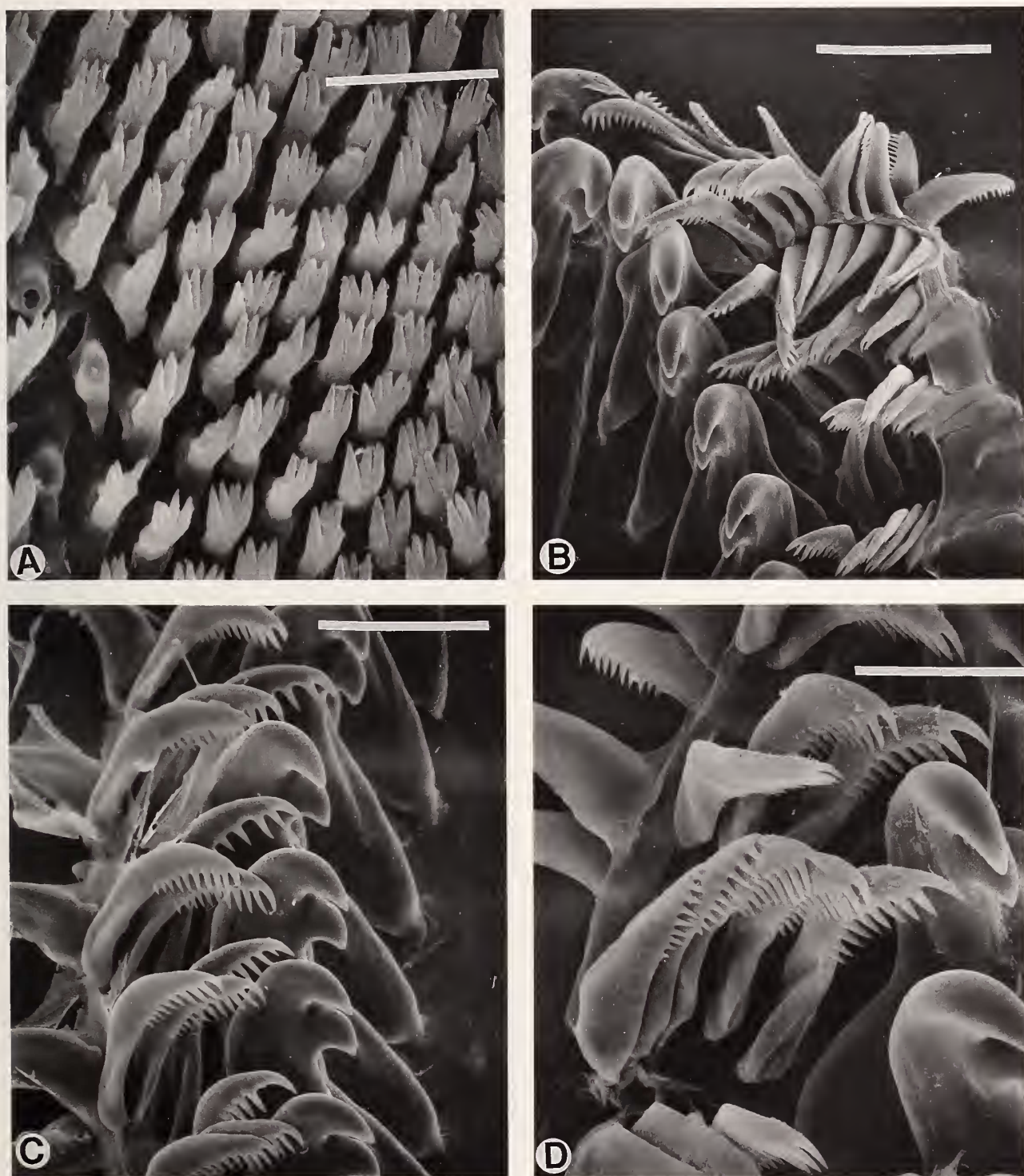


Figure 25

Hallaxa hileenae Gosliner & Johnson, sp. nov. Scanning electron micrographs, CASIZ 086402. A. Jaw rodlets, scale = 15 μm . B. Half row of radular teeth, scale = 60 μm . C. Inner and outer lateral teeth, scale = 43 μm . D. Outer lateral teeth, scale = 25 μm .

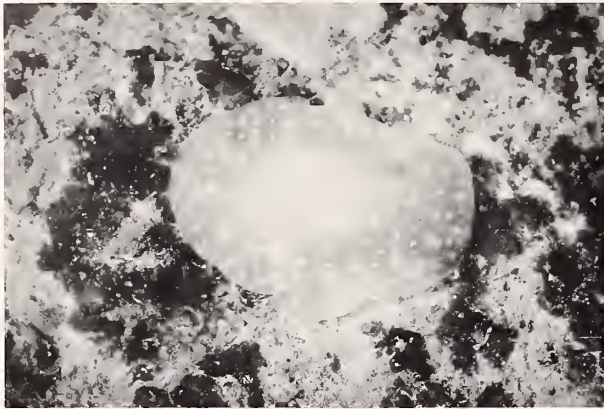


Figure 26

Hallaxa cryptica Gosliner & Johnson, sp. nov. Living animal of white color form, Philippines.

Kwajalein Atoll, Marshall Islands, 8 m depth, 19 September 1982, S. Johnson. One specimen (white form), CASIZ 088351, Enewetak Atoll, Marshall Islands, 16 September 1982, S. Johnson. Two specimens (white form), one dissected, CASIZ 088352, Enewetak Atoll, Marshall Islands, 30 July 1983, S. Johnson. One specimen (white form), dissected, CASIZ 088353, Enewetak Atoll, Marshall Islands, 5 November 1988, S. Johnson.

Distribution: This species has been collected from the Marshall Islands and the Philippine Islands.

Etymology: The name *cryptica* refers to the cryptic coloration of this species on its sponge prey.

External morphology: The living animals are 7–25 mm in length with a rounded body shape. The general body color is variable and may be either creamy yellowish white (Figure 26A) or, less commonly, light purple brown (Figure 1G). The purple form may have darker purple flecks. Both forms have scattered opaque white spots that appear

as tubercles, but are not elevated from the notum. Whitish specimens may also have light tan streaks and spots perpendicular to the notal margin. The rhinophores and gills are the same color as, or slightly darker than, the general body color. Purple specimens have a white tip at the apex of the rhinophores. The branchial plumes consist of 8–15 unipinnate gills. The rhinophores are bulbous with five to nine lamellae. The foot (Figure 27A) is concavely curved anteriorly with broad, anteriorly directed foot corners. A small pit is present at the lateral margins of the mouth and head.

Internal morphology: The buccal mass consists of a short muscular region and a more elongate, anterior glandular region. The labial cuticle consists of a ring of jaw elements at the anterior end of the muscular portion of the buccal mass. The jaw elements (Figure 28A) consist of numerous rows of rodlets, each with one to three denticles along its margin. The radular formula in two purple specimens is $21 \times 9-10.1.0.1.9-10$ and $25 \times 7.1.0.1.7$, and $34 \times 14.1.0.1.14$ (Figure 28B) in the one white specimen examined. The inner lateral teeth (Figures 28C, D, 29A) are broad and thick in specimens of both color forms. The inner edge of the free portion of the inner laterals is curved and bifid, without secondary denticles. The outer lateral teeth are narrow basally, and elongate. The outermost teeth are shorter than the more inner ones. The outer laterals bear 6–12 denticles along their inner margin (Figure 29B).

The reproductive system (Figure 27B) is triaulic. The pre-ampullary duct widens to a broad, saccate ampulla. The ampulla narrows and bifurcates into the short oviduct and the vas deferens. The vas deferens widens into the proximal prostatic portion. This prostatic segment curves and narrows into the straight, muscular ejaculatory portion. The ejaculatory segment exits at the gonopore, adjacent to the vagina. The vagina is thin and elongate. It joins the base of the duct of the pyriform receptaculum seminis. These ducts join with the short uterine duct and

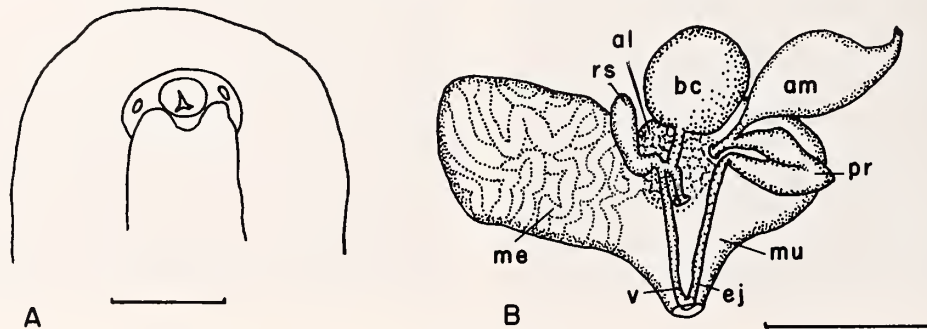


Figure 27

Hallaxa cryptica Gosliner & Johnson, sp. nov. A. Camera lucida line drawing of ventral view of head and foot of preserved specimen, scale = 1.0 mm. B. Reproductive system, al- albumen gland, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 0.75 mm.

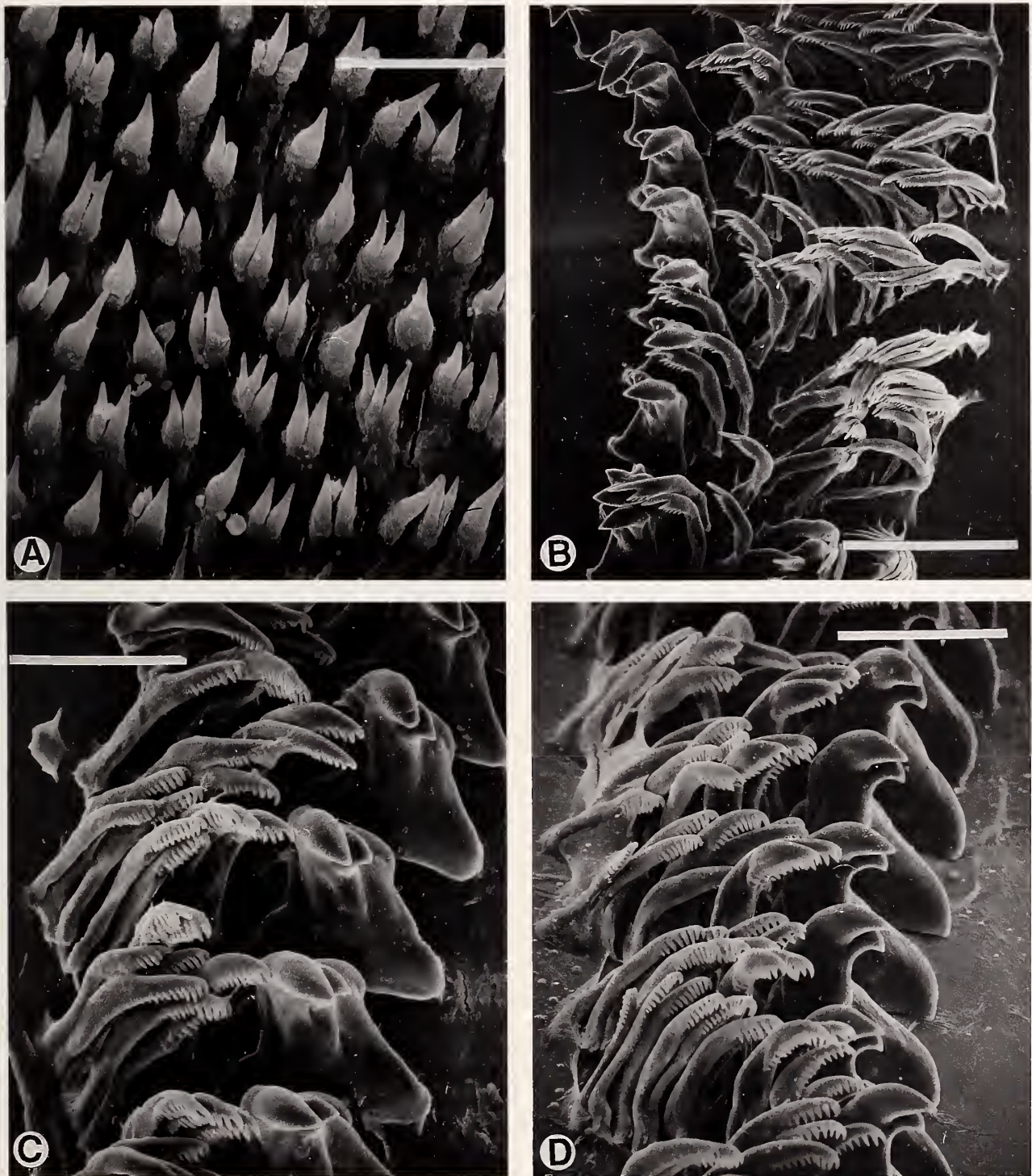


Figure 28

Hallaxa cryptica Gosliner & Johnson, sp. nov. Scanning electron micrographs. A. Jaw rodlets, purple specimen, Philippines, CASIZ 083764, scale = 15 μ m. B. Half row of teeth, white specimen, Enewetak, CASIZ 088352, scale = 100 μ m. C. Half row of teeth, purple specimen, Enewetak, BPBM 9941, scale = 60 μ m. D. Half row of teeth, purple specimen, Philippines, CASIZ 083764, scale = 60 μ m.

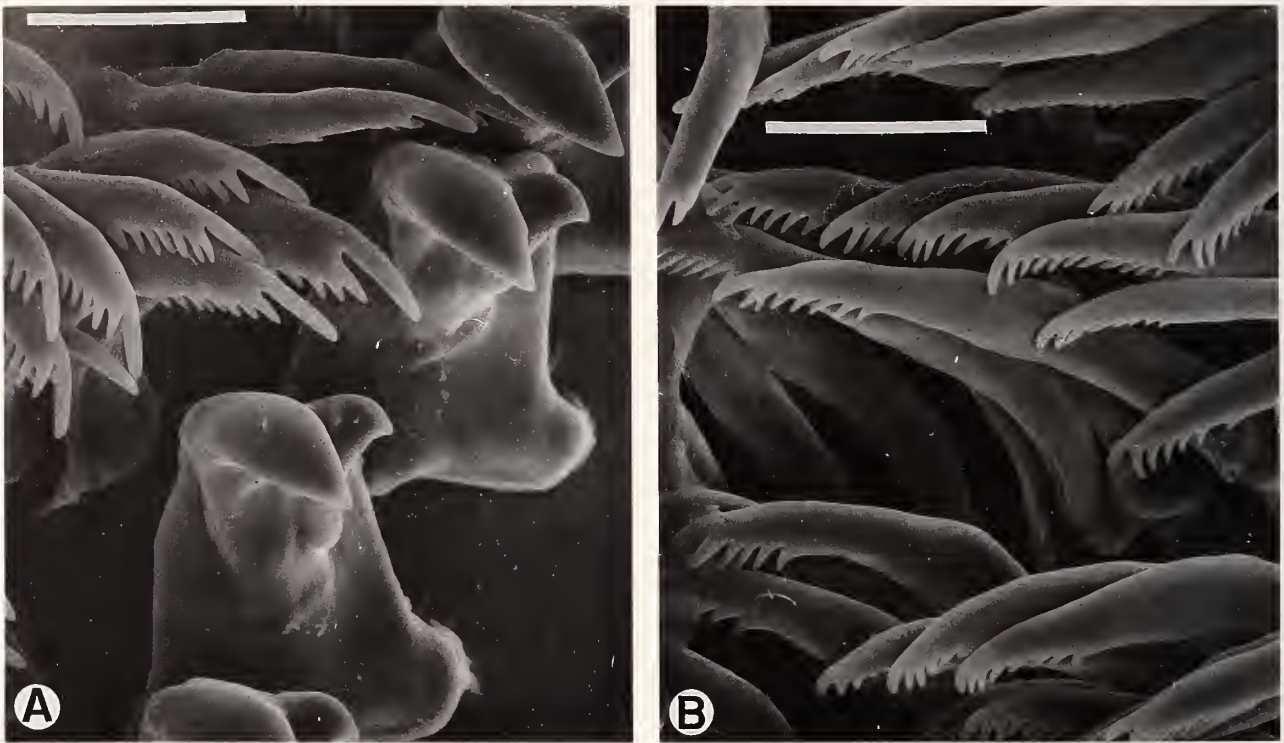


Figure 29

Hallaxa cryptica Gosliner & Johnson, sp. nov. Scanning electron micrographs. A. Inner lateral teeth, white specimen, Enewetak, CASIZ 088352, scale = 30 μ m. B. Outer lateral teeth, white specimen, Enewetak, CASIZ 088352, scale = 30 μ m.

the slightly longer duct of the bursa copulatrix. The bursa is large, thin-walled, and spherical. The uterine duct enters the female gland mass within the albumen gland. The mucous gland is large with numerous tubercles. It is a distinct lobe, separated laterally from the albumen and membrane glands.

Discussion: There are no apparent differences, either external or internal, between purple and white specimens, other than those relating to color. *Hallaxa cryptica* is most similar to *H. translucens* and *H. paulinae* in general appearance. All three species are cryptic in appearance and have a broad body shape, but differ in important aspects of their anatomy. These differences are discussed in detail in the discussions of the two other taxa. The anatomy of the reproductive system suggests closer affinities of *H. cryptica* to *H. indecora*, *H. hileenae* and *H. michaeli* than to *H. translucens* or *H. paulinae*. *H. cryptica*, *H. indecora*, *H. hileenae* and *H. michaeli* have a lobed membrane gland that is well-separated from the remainder of the female gland mass.

Hallaxa michaeli Gosliner & Johnson, sp. nov.

(Figures 1H, 30, 31)

Hallaxa indecora Burn, 1958:27, not Bergh, 1905.

Material: Holotype, AM C.174884, Bateman's Bay, New South Wales, Australia, intertidal, 19 December 1984, M. L. Gosliner.

Distribution: This species is known from the type locality in New South Wales and Victoria (Burn, 1958), Australia.

Etymology: This species is named for Michael Gosliner, who collected the holotype specimen of this species.

External morphology: The living specimen (Figure 1H) is 6 mm in length, elongate and ovoid in shape. It is uniformly dirty translucent yellowish white with a few scattered opaque white specks. The notum is smooth and devoid of tubercles. The apex of the rhinophores is also opaque white. There are nine unipinnate gills and seven lamellae on either rhinophore. The foot (Figure 30A) is rounded anteriorly with broad, triangular, anteriorly directed foot corners. A pit is present near the lateral margin of either side of the head.

Internal morphology: The buccal mass is elongate with the anterior portion being highly glandular. The labial cuticle consists of numerous multifid rodlets (Figure 31A). The radular formula in the single specimen is $27 \times 6-8.1.0.1.6-8$ (Figure 31B, C). The inner lateral teeth (Figure 31D) are broad and thick. Their free edge contains a pair of curved cusps. No auxiliary denticles are present.

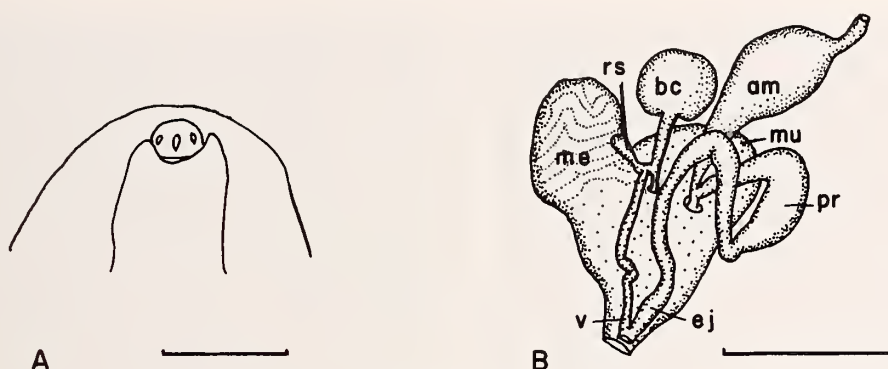


Figure 30

Hallaxa michaeli Gosliner & Johnson, sp. nov. A. Camera lucida line drawing of ventral view of head and foot of preserved specimen, scale = 1.0 mm. B. Reproductive system, am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, me- membrane gland, mu- mucous gland, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, scale = 1.0 mm.

The outer lateral teeth (Figure 31B, C) are narrow and elongate with the outermost teeth being slightly shorter than the inner ones. The innermost outer laterals have 9–10 triangular denticles on their inner face. The outermost ones have six to eight denticles.

The reproductive system (Figure 30B) is triaulic. The narrow pre-ampullary duct widens to a short, thick ampulla. The ampulla narrows and bifurcates into the short oviduct and the vas deferens. The proximal part of the vas deferens is prostatic. It curves and narrows into the ejaculatory portion. The ejaculatory segment is elongate and forms one elongate loop. It terminates at the gonopore, adjacent to the vagina. The vagina is elongate and slightly convoluted. It joins the small, digitiform receptaculum seminis. Together these ducts join the short uterine duct and more elongate duct of the bursa copulatrix, after a short distance. The membrane gland consists of many tubules and is a lobe distinct from the albumen and mucous glands.

Discussion: Burn (1958) described the external morphology of the specimen from Victoria, Australia, which he called *Hallaxa indecora* Bergh. The pale yellow body color is similar to the type specimen of *H. michaeli*. The remaining features of gill and rhinophoral lamellae number are similar to those described here. Burn also described the presence of structures on the sides of the mouth that he thought might be degenerate oral tentacles. These agree with the vestigial tentacular pits described here for *H. michaeli* (Figure 27A). It is highly likely that Burn's specimen is *H. michaeli*, but this must be verified by examination of its internal anatomy.

Despite the fact that only a single specimen of this species was examined, it is sufficiently distinct to warrant description. It differs in its coloration from the other species that have only two large cusps without secondary denticles on the inner lateral teeth. *Hallaxa cryptica* may also be whitish in color, but it has large opaque white spots, a

broader body, and more elongate outer lateral teeth. *Hallaxa michaeli* is unique in having a more elongate vas deferens than other members of the genus.

DISCUSSION

A. Significance to doridaean phylogeny

Cryptobranchs are dorid nudibranchs that have the derived feature of possessing a circle of gills that can be withdrawn into a branchial cavity below the surface of the mantle. Other groups of dorids have a circle of gills, but they cannot be withdrawn into a protective pocket. Phanerobranchs and gnathodorids (*Bathydoris* and *Doridoxa*) have plesiomorphically thickened, chitinous jaws with or without jaw rodlets, while the cryptobranchs have more derived jaws reduced to a small area that may contain some chitinous rodlets. Wägele (1989) has suggested that bathydorids may be the sister taxon of the remainder of the Doridacea. Certainly, detailed analysis of nudibranch phylogeny, using a wide array of features, is needed to shed more light on dorid phylogeny. This requires more detailed examination of doridaeans as well as less derived members of the outgroups of dorids, dendronotaceans, arminaceans, aeolidaceans, and notaspideans.

The systematics of the cryptobranch dorid nudibranchs has been the source of controversy and disagreement since Bergh (1892) presented his classification of the Nudibranchia. Other classifications have been suggested, including the works of Thiele (1931) and Franc (1968). Kay & Young (1969) considered a series of dorid subfamilies, based on anatomical and ecological information. However, their treatment was restricted to dorid taxa present in the Hawaiian Islands. There have been few major monographic revisions of large groups of cryptobranch dorids in the last half century. An exception is the review of the kentrodorid genera *Kentrodoris* and *Jorunna* (Ev. Marcus, 1976).

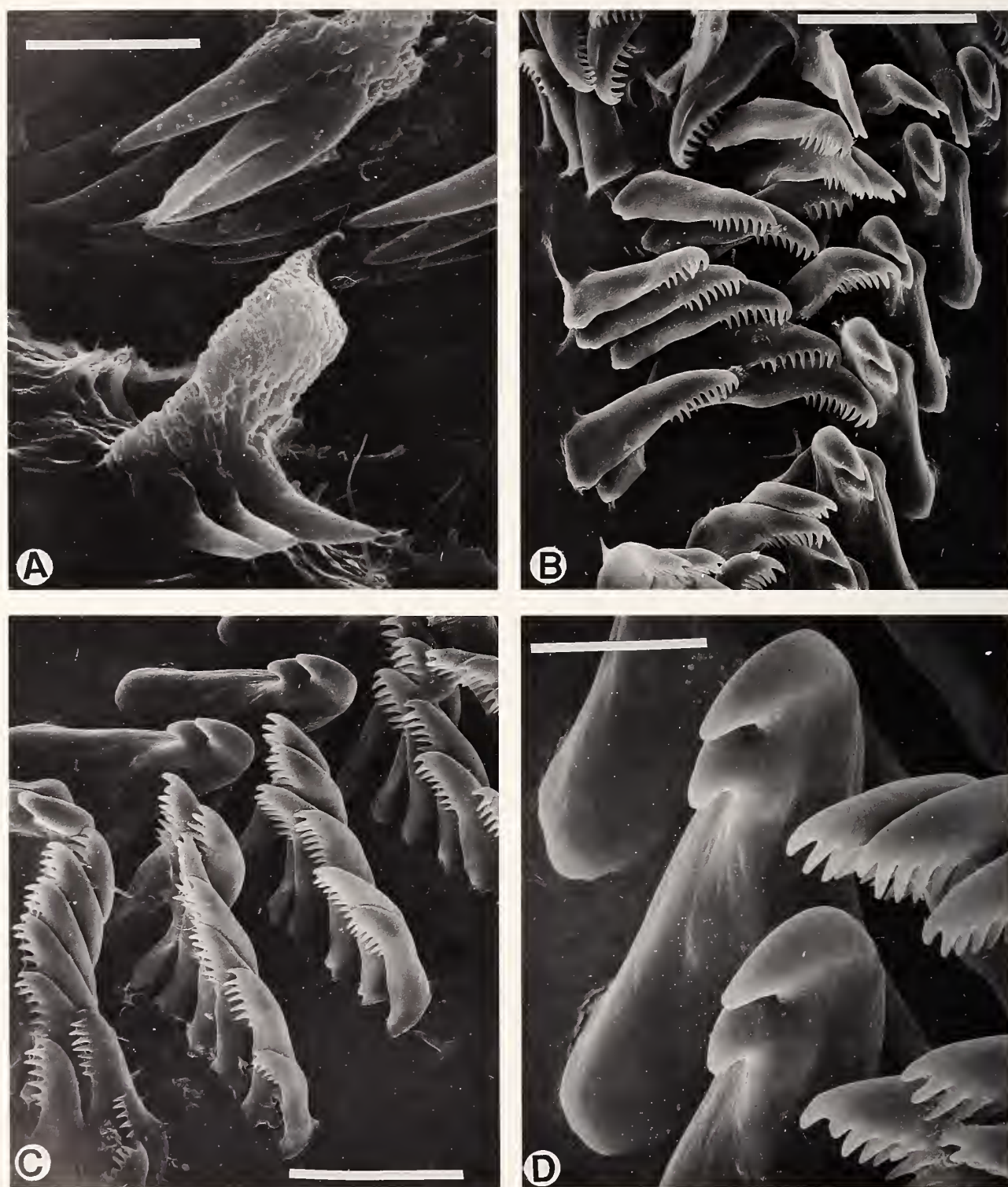


Figure 31

Hallaxa michaeli Gosliner & Johnson, sp. nov. Scanning electron micrographs, holotype, CASIZ 071472. A. Jaw rodlets, scale = 5 μm . B. Half row of radular teeth, scale = 38 μm . C. Half row of radular teeth, scale = 30 μm . D. Inner lateral tooth, scale = 13.6 μm .

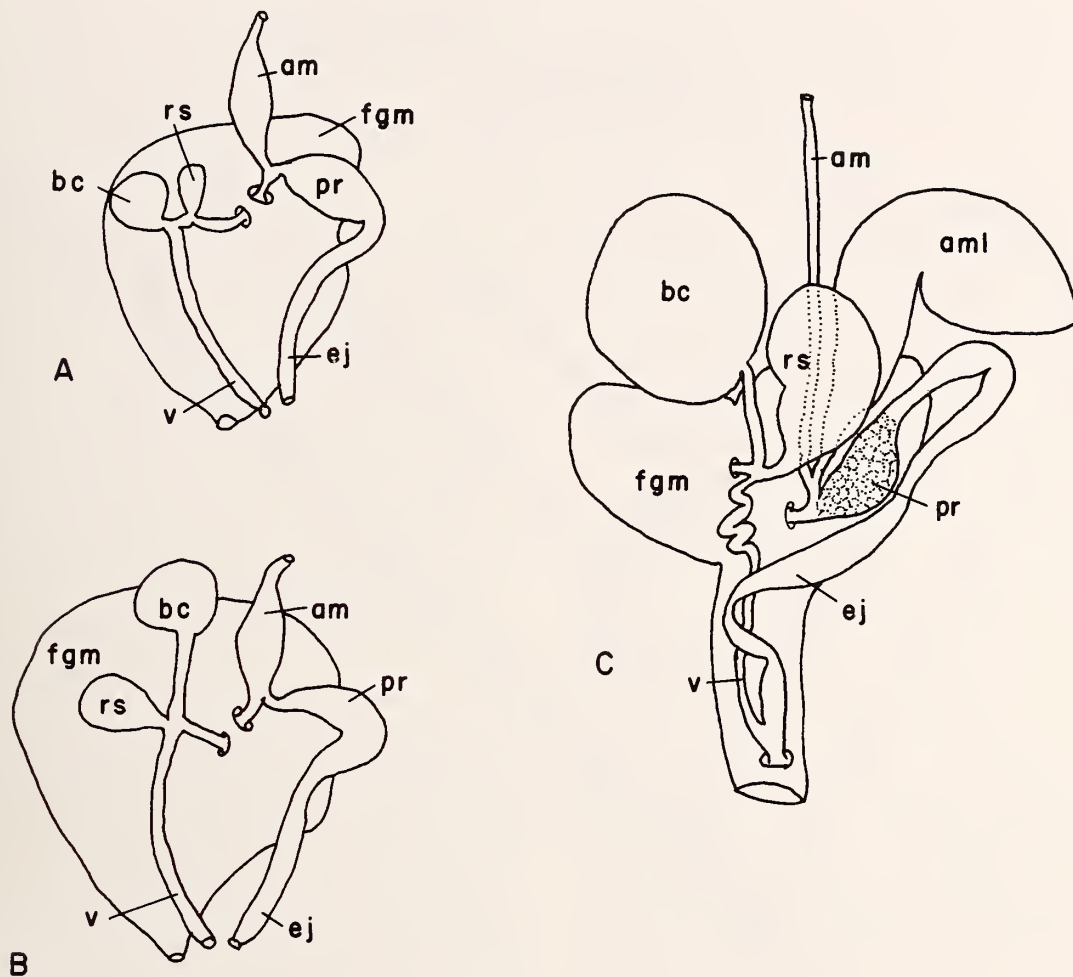


Figure 32

Dorid reproductive systems. A. Cryptobranch with serial arrangement. B. *Hallaxa* with semi-serial arrangement. C. *Actinocyclus japonicus* (Eliot, 1913), with semi-serial arrangement. am- ampulla, bc- bursa copulatrix, ej- ejaculatory portion of vas deferens, mu- mucous gland, fg- female gland mass, pr- prostatic portion of vas deferens, rs- receptaculum seminis, v- vagina, not to scale.

The first comprehensive treatment of cryptobranch dorids in recent times is the generic revision of the Chromodorididae undertaken by Rudman (1984). He evaluated polarities of evolutionary change in chromodorids and revised the generic distinctions, but did not evaluate the limits of genera based on strictly cladistic methodology. He studied polarity of character evolution in chromodorids, but did not evaluate whether the genera he circumscribed were monophyletic or diagnosed on the bases of synapomorphic features. Nevertheless, Rudman's treatment of chromodorid classification represents the first comprehensive treatment of dorid classification employing a wide variety of characters from different organ systems.

In his discussion of dorid evolution, Rudman noted that chromodorids are unique in their arrangement of reproductive organs. Virtually all other dorids have a serial arrangement of reproductive organs. In this configuration,

the uterine duct connects to the receptaculum seminis and joins the receptaculum to the base of the bursa copulatrix (Figure 32A). The vagina emerges from the base of bursa and exits at the gonopore, adjacent to the penis. This is the plesiomorphic arrangement within the dorids and is also present in most notaspideans (Willan, 1987), the likely sister taxon of the Doridacea. In chromodorids, the duct from the receptaculum enters the mid-region of the vagina. An arrangement of reproductive organs similar to that of chromodorids is found in several species of *Hallaxa* (Figure 32B) and *Actinocyclus japonicus* (Eliot, 1913) (Figure 32C). In these taxa, the uterine duct joins the middle of the vaginal duct. This is a derived feature shared only by members of the Chromodorididae and Actinocyclidae. Contrary to most other dorids, members of these taxa also are known to feed largely upon sponges that lack spicules (Rudman, 1984; Goddard, 1984). The radulae of chro-

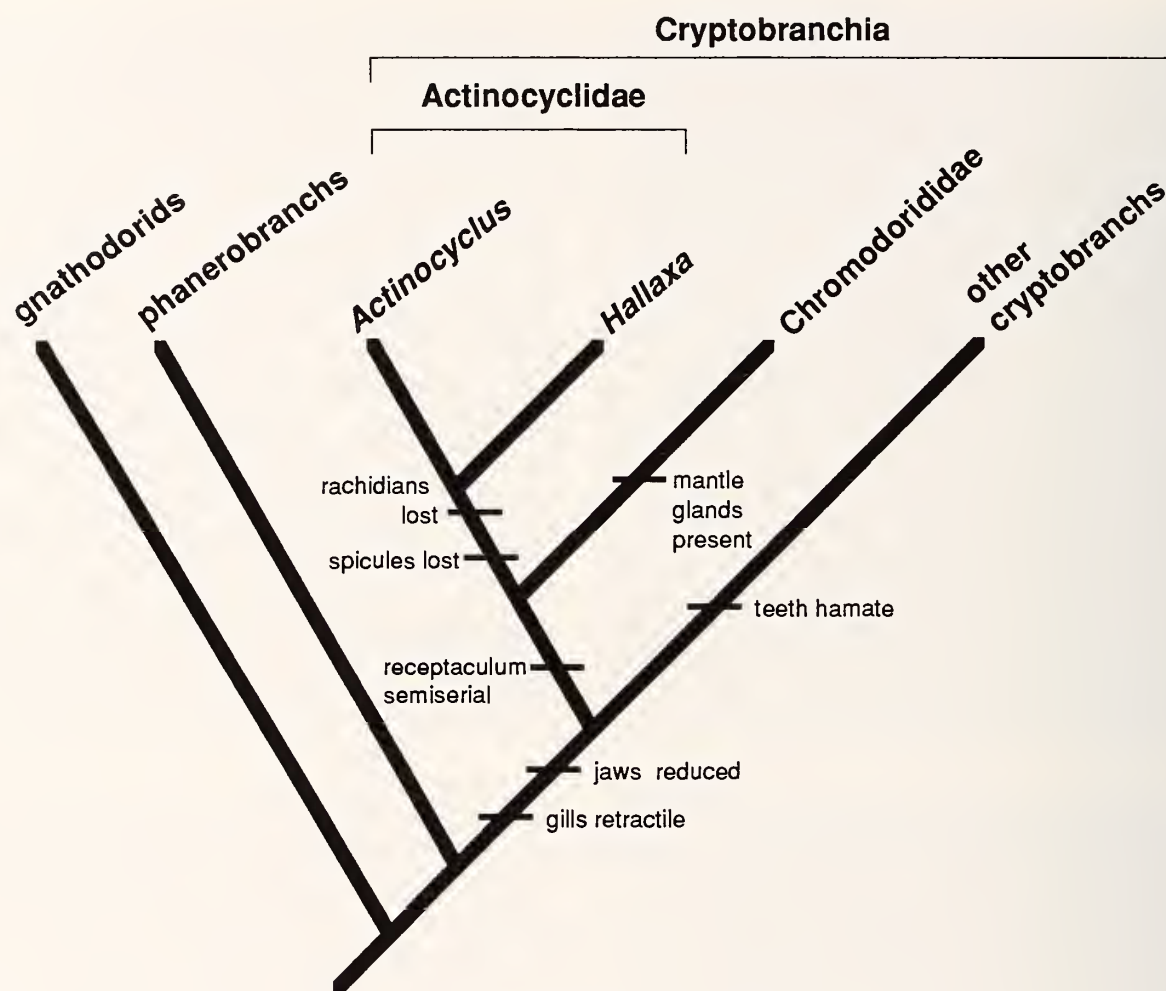


Figure 33

Hypothesized phylogeny of Doridacea.

modorids and actinocyclids are similar in having a large primary cusp with numerous smaller denticles along the margins of the teeth. This form of radular teeth also appears to be derived rather than ancestral, based upon out-group comparisons with phanerobranch and gnathodorid dorids and notaspideans. The remainder of the cryptobranchs have simply hamate teeth, which appears to represent another derived form when compared to outgroups. Based on their similar derived reproductive and radular morphology, it appears that chromodorids and actinocyclids are more closely related to each other than to any other cryptobranch dorids. Rudman also demonstrated that many chromodorids retain a rachidian row of teeth; this is a plesiomorphic arrangement within the chromodorids. Species of *Bathydoris* (Wägele, 1989) and some phanerobranchs also have a rachidian row of teeth, and this appears to represent the plesiomorphic arrangement within the Doridacea. The fact that the vestiges of rachidian teeth are found only in some chromodorids, but not in any other

cryptobranchs, suggests that the chromodorid-actinocyclid clade is divergent from the remainder of the Cryptobranchia. Most other systematic treatments have considered chromodorids and actinocyclids as highly derived cryptobranchs. Chromodorids have well-developed dermal defensive glands that are unique to members of this taxon. Actinocyclids share two derived features absent in the least derived members of their sister group, the Chromodorididae; the rachidian teeth are absent and the notum lacks spicules. The phylogenetic hypothesis suggested here for cryptobranch dorid nudibranchs is summarized in Figure 33.

B. Morphological variability and character polarity

Few morphological studies have been undertaken within the Actinocyclidae. The only description of reproductive morphology of a species of *Actinocyclus* is that of *A. japonicus* (Eliot, 1913) by Kay & Young (1969). Specimens of *A. japonicus* and three previously described species of

Hallaxa, *H. apesae*, *H. chani*, and *H. indecora* were examined to confirm described morphological variability. Morphology of *H. gilva* and *H. decorata* were based only upon their original descriptions.

In order to ascertain the polarity of morphological change within *Hallaxa*, *Actinocyclus* and chromodorids were considered as outgroups.

The following characters were considered:

1. Gills: Within the Actinocyclusidae, all taxa possess unipinnate gills. There are 8–18 gills in *Actinocyclus japonicus* and 6–14 in species of *Hallaxa*. Several species have more gills than others, independent of their relative body size. A larger number of gills is considered plesiomorphic, based on comparisons with *Actinocyclus*. It appears that the plesiomorphic arrangement of the gills in the Chromodorididae is bi-tripinnate gills.

0 = 12–15 gills; 1 = 6–11 gills.

2. Body shape: In *Hallaxa*, some specimens have a round, ovoid body shape, while others are far narrower and more elongate. Species of *Actinocyclus* and less derived chromodorids are round in shape. This shape is considered plesiomorphic for *Hallaxa*.

0 = round body shape; 1 = ovoid to elliptical body shape.

3. Tubercles: Species of *Actinocyclus* and some *Hallaxa* have large rounded tubercles scattered over the surface of the notum. These tubercles do not appear to be supported by spicules. Other species of *Hallaxa* have either small tubercles or an entirely smooth notum. Possessing large tubercles is considered plesiomorphic in *Hallaxa*, with small tubercles being derived from large, and a smooth notum derived from one with small tubercles. A few chromodorids of the least derived genera *Cadlina* and *Tyrinna* have many large tubercles. This appears to be an ordered character with the following transformation series 0–1–2.

0 = many, large tubercles; 1 = few small tubercles; 2 = smooth notum.

4. Rhinophoral lamellae: In *Actinocyclus*, chromodorids, and most species of *Hallaxa*, the rhinophoral lamellae are simple ridges, extending a short distance out from the clavus. In *H. iju*, the lamellae extend outwards for at least twice the distance of those of other species. This elaboration is considered autapomorphic.

0 = short lamellae; 1 = extended lamellae.

5. Rhinophoral shape: The majority of dorid nudibranchs, including the Chromodorididae, *Actinocyclus* and *Hallaxa*, have bulbous rhinophores. *Hallaxa paulinae* is unique in having conical rhinophores with few lamellae. This is considered as an autapomorphy for *H. paulinae*.

0 = bulbous rhinophores; 1 = conical rhinophores.

6. Oral tentacles: In *Actinocyclus* and chromodorids, a short oral tentacle is present on either side of the mouth. Its form is variable in chromodorids (Rudman, 1984), but either grooved or digitiform tentacles are present in all taxa. In some species of *Hallaxa*, reduced oral tentacles

may be present, or a small pit may be found on either side of the head. These pits are considered to represent vestiges of the oral tentacles and represent a derived condition within the Actinocyclusidae.

0 = oral tentacles present; 1 = oral pits present.

7. Foot: In chromodorids and most other cryptobranch dorids, the anterior margin of the foot is slightly rounded with the anterolateral margins extending laterally. This form is also present in some species of *Hallaxa*. In the remaining species of *Hallaxa*, the lateral margins of the foot are directed anteriorly. Species of *Actinocyclus* have an arrangement of the foot similar to that found in the species of *Hallaxa* with anteriorly directed foot margins. However, in *Actinocyclus*, the margins almost entirely surround the mouth and oral tentacles. Also, there appears to be a secondary thickening near the anterior margin of the foot. A straight foot appears to be the ancestral condition in *Hallaxa* and most other dorids. Subsequent character analysis indicates that the derived forms present in some species of *Hallaxa* and *Actinocyclus* represent independently derived modifications of the ancestral configuration and are here treated as unordered.

0 = straight foot margin; 1 = concave foot margin; 2 = rounded foot margin with thickening.

8. Jaw armature: All chromodorids and all species of *Actinocyclus* and *Hallaxa* have a pair of narrow bands of rodlets along the anterior margin of the labial cuticle. In *Hallaxa* sp., there are only three to four rows of rodlets forming a thin band of armature along the jaws. All other species have multiple rows (at least 10), which is considered plesiomorphic for the chromodorid-actinocyclusid clade. A reduced number of rows of rodlets is autapomorphic for *Hallaxa* sp.

0 = more than 10 rows of rodlets; 1 = 3–4 rows of rodlets.

9. Jaw rodlets: In species of *Actinocyclus* and some species of *Hallaxa*, the jaw rodlets are simple, undivided hooks. Most chromodorids have divided rodlets. In most species of *Hallaxa*, the rodlets have multifid apices. This latter form is considered the derived form within the Actinocyclusidae.

0 = undivided rodlets; 1 = divided rodlets.

10. Outer lateral teeth: The radula of most chromodorids and *Actinocyclus* is broad, with numerous lateral teeth per row. In *Actinocyclus*, there are 20–30 outer lateral teeth on either side of the radula. In contrast, species of *Hallaxa* have 4–22 outer lateral teeth per half row. Species with fewer outer lateral teeth are considered to be more derived than species with many teeth.

0 = 13–22 outer laterals/side; 1 = 4–11 outer laterals/side.

11. Outer lateral shape: In chromodorids, *Actinocyclus*, and most species of *Hallaxa*, the outer lateral teeth are all comb-shaped. *Hallaxa elongata* is unique in having outer

lateral teeth that are similar to the inner lateral teeth in shape. This is considered to represent an autapomorphy in *H. elongata*.

0 = comb-shaped outer laterals; 1 = cuspidate outer laterals.

12. Inner lateral cusp: The inner lateral teeth of species of *Actinocyclus* and some species of *Hallaxa* have a single rounded-to-pointed cusp with small denticles along the outer side of the tooth. In other species of *Hallaxa*, the bifid primary cusp is bifid and planar on the inner edge of the tooth. This planar, bifid cusp is considered apomorphic within the Actinocyclusidae. A bifid cusp is present in the highly derived chromodorid genus *Hypselodoris* and other species of *Hallaxa*. The bifid cusp in these taxa is not planar and appears to have originated independently.

0 = multiplanar cusps; 1 = bifid, planar cusp.

13. Inner lateral shape: Species of *Actinocyclus* and most species of *Hallaxa* have inner lateral teeth that are markedly broader than the adjacent outer lateral teeth. This is also true of many chromodorids in the genera *Cadlina* and *Noumea*. In *H. sp.* the inner lateral teeth are thin and not markedly different from the outer laterals. This appears to be an autapomorphy for *H. sp.*

0 = inner lateral broad; 1 = inner lateral narrow.

14. Inner lateral dentition: The inner lateral teeth of most chromodorids, *Actinocyclus*, and most species of *Hallaxa* have smaller denticles on the outside of the primary cusp. In several species of *Hallaxa* with a bifid, planar cusp on the inner lateral teeth, secondary denticles are entirely absent. This is considered a derived feature.

0 = secondary denticles present; 1 = secondary denticles absent.

15. Receptaculum seminis: In many chromodorids, *Actinocyclus*, and some species of *Hallaxa*, the receptaculum seminis is situated immediately opposite the point where the uterine duct enters the vagina. The receptaculum seminis is situated more distally in other species of *Hallaxa*. This later form is considered apomorphic.

0 = receptaculum opposite uterine duct; 1 = receptaculum situated off vagina, distal to uterine duct.

16. Vagina: In chromodorids, *Actinocyclus*, and most species of *Hallaxa*, the vaginal duct is elongate and the uterine duct joins it near the middle of its length. The uterine duct of *H. paulinae* enters the vagina far more distally. The receptaculum seminis enters the vagina even more distally, close to the common gonopore. This arrangement is considered to be autapomorphic for *H. paulinae*.

0 = uterine duct enters middle of vagina; 1 = uterine duct enters distal portion of vagina.

17. Prostate: The vas deferens of *Actinocyclus japonicus* was described as showing no hint of a prostatic portion (Kay & Young, 1969). Two specimens examined here have a distinct prostate, restricted to the proximal end of the vas deferens (Figure 29D). All chromodorids and species

of *Hallaxa* examined have an elongate prostate that occupies the proximal third to half of the vas deferens. A prostate restricted to the proximal end of the vas deferens is found in many species of notaspideans (Ev. Marcus & Gosliner, 1984; Willan, 1987). It appears that the more restricted prostate of *Actinocyclus* is plesiomorphic for the family and that the more distal prostate of *Hallaxa* and chromodorids represent apomorphic conditions.

0 = prostate restricted to base of vas deferens; 1 = prostate found throughout proximal portion of vas deferens.

18. Vas deferens: The ejaculatory portion of the vas deferens is relatively short and straight in *Actinocyclus* and most species of *Hallaxa*. In *H. michaeli*, the ejaculatory portion is curved and more elongate. This is considered the derived condition within the Actinocyclusidae and is autapomorphic in *H. michaeli*.

0 = ejaculatory vas deferens short; 1 = ejaculatory vas deferens long.

19. Membrane gland: In chromodorids, *Actinocyclus*, and several species of *Hallaxa*, the membrane gland is adjacent to the albumen and mucous glands. In some species of *Hallaxa*, the membrane gland is separated from the albumen and membrane glands as a discrete lobe. This is considered to represent the derived condition within the Actinocyclusidae.

0 = membrane gland continuous with rest of female gland mass; 1 = membrane gland a separate lobe.

20. Ampulla: In virtually all dorids that have been studied, the ampulla is a serial tube with expanded width for storage of endogenous sperm. This is certainly true of the presumed sister groups of the Actinocyclusidae, the Chromodorididae, and all species of *Hallaxa* examined. In two specimens of *Actinocyclus japonicus* examined here, a narrow hermaphroditic duct bifurcates into the oviduct and vas deferens. Also inserting into this junction is a thick sac that stores endogenous sperm. This sac functions as the ampulla, but is separate from the hermaphroditic duct. This represents a derived feature within the Actinocyclusidae.

0 = only primary ampulla present; 1 = primary and secondary ampullae present.

C. Cladistic relationships within Actinocyclusidae

In order to develop hypotheses regarding the phylogeny of the Actinocyclusidae, the above described characters were placed in a data matrix (Table 1) and analyzed using Phylogenetic Analysis Using Parsimony, versions 2.4.1 and 3.1.1, by David Swofford. Twenty-two most parsimonious trees were produced. A consensus tree is depicted for these taxa (Figure 34). In this arrangement, a tree with a length of 38 steps and a consistency index of 0.579 was produced. In this phylogenetic hypothesis, five of the 20 characters exhibit at least one instance of reversal. These include number of gills, general body shape, dentition of the jaw rodlets, number of outer lateral teeth, and position

Table 1
Morphology of Actinocyclusidae.

	Gills	Body shape	Tubercles	Rhinophoral lamellae	Rhinophoral shape	Oral tentacles	Foot	Jaw armature	Jaw rodlets	Outer lateral teeth	Outer lateral shape	Inner lateral cusp	Inner lateral shape	Inner lateral dentition	Receptaculum seminis	Vagina	Prostate	Vas deferens	Membrane gland	Ampulla
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>A. japonicus</i>	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>H. aephae</i>	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0
<i>H. chani</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
<i>H. atrotuberculata</i>	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>H. iju</i>	1	1	1	1	0	0	1	0	1	1	0	0	0	0	1	0	1	0	0	0
<i>H. elongata</i>	1	1	1	0	0	1	1	0	0	1	1	0	0	0	1	0	1	0	0	0
<i>H. albopunctata</i>	1	1	1	0	0	1	1	0	1	1	0	0	0	0	0	0	1	0	0	0
<i>H. sp.</i>	1	1	2	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0
<i>H. indecora</i>	1	1	2	0	0	1	1	0	1	1	0	1	0	1	1	0	1	0	1	0
<i>H. hilleenae</i>	1	1	2	0	0	1	1	0	1	1	0	1	0	1	1	0	1	0	1	0
<i>H. cryptica</i>	0	0	2	0	0	1	1	0	1	0	0	1	0	1	1	0	1	0	1	0
<i>H. paulinae</i>	1	0	2	0	1	1	1	0	1	1	0	0	0	0	1	1	1	0	0	0
<i>H. michaeli</i>	1	1	2	0	0	1	1	0	1	1	0	1	0	1	1	0	1	1	1	0
<i>H. gilva</i>	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0
<i>H. translucens</i>	0	0	2	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0
Character number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20

of the receptaculum seminis. Three characters—body shape, loss of tubercles, and the shape of the anterior margin of the foot—exhibit one or more instances of parallelism. Seven characters are autapomorphic. The pentachotomy depicted in the consensus tree of *H. chani*, *H. translucens*, *H. gilva* and *H. atrotuberculata* is the result of ambiguities in the sequence of changes in body shape, foot shape, and jaw rodlets. One additional quadrichotomy and one trichotomy are present. Further investigation is required to resolve the ambiguities.

D. Systematic relationships

Considerable discussion has focused on the distinction between *Hallaxa* and *Actinocyclus* (Thiele, 1931; Marcus, 1957; Franc, 1968; Gosliner & Williams, 1975; Miller, 1987). Gosliner & Williams reviewed all the characters mentioned and noted that *Actinocyclus* has more rows of radular teeth, a less variable inner lateral tooth, and a broader body and foot than *Hallaxa*. Miller added that *Hallaxa* has multifid jaw rodlets and the posterior end of the foot extends beyond the posterior limit of the notum. With the study of additional species, it is apparent that these distinctions should be reexamined. Species of *Actinocyclus* clearly have almost twice the number of radular rows than any species of *Hallaxa* thus far studied. The only possible exception to this is the original description of *H. indecora*, where Bergh (1905) indicated that it had

60–65 rows of radular teeth. As indicated in the above discussion of this species, this record is dubious. The contention that the inner lateral teeth of *Actinocyclus* are less variable than those of *Hallaxa* cannot be maintained. This appears to be a species-specific character. Species of *Actinocyclus* have a consistently broader body, with more circular shape than species of *Hallaxa*. Miller's statement that *Hallaxa* species have multifid rodlets, while species of *Actinocyclus* have undivided ones, is contradicted by the presence of undivided rodlets in *H. atrotuberculata*, *H. sp.*, and *H. elongata*. It does appear that the free end of the foot of most species of *Hallaxa* extends posteriorly beyond the notum, though this is not always evident in somewhat contracted individuals. None of the above features used to distinguish the genera is apomorphic within *Actinocyclus*. All represent derivations within *Hallaxa*. This would suggest that *Actinocyclus* is paraphyletic and should not be maintained as a distinct genus. From the analysis presented here, it is apparent that *Actinocyclus* has two apomorphic features that distinguish it from *Hallaxa*, an elaboration of the anterior portion of the foot and a secondary ampulla next to the hermaphroditic duct. In addition to the above mentioned apomorphies for *Hallaxa*, the presence of an elongate prostatic portion of the vas deferens is a derived feature that distinguishes *Hallaxa* from *Actinocyclus*. It is thus concluded that both *Actinocyclus* and *Hallaxa* represent distinct monophyletic taxa.

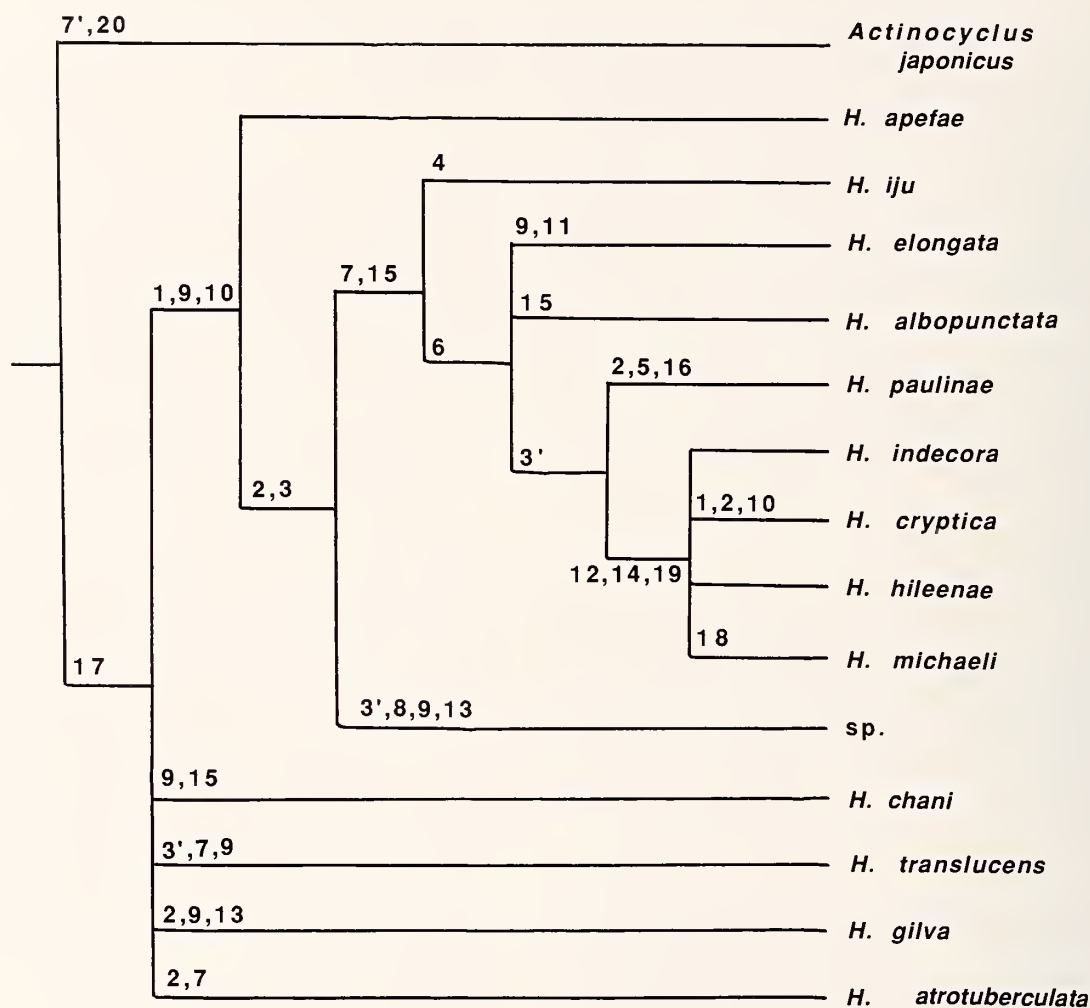


Figure 34

Hypothesized phylogeny of *Hallaxa*.

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